



Gynoecium structure in Sapindales and a case study of *Trichilia pallens* (Meliaceae)

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Abstract

Sapindales is a monophyletic order within the malvid clade of rosids. It represents an interesting group to address questions on floral structure and evolution due to a wide variation in reproductive traits. This review covers a detailed overview of gynoecium features, as well as a new structural study based on *Trichilia pallens* (Meliaceae), to provide characters to support systematic relationships and to recognize patterns of variations in gynoecium features in Sapindales. Several unique and shared characteristics are identified. Anacrotylous and basistylous carpels may have evolved multiple times in Sapindales, while ventrally bulging carpels are found in pseudomonomerous Anacardiaceae. Different from previous studies, similar gynoecium features, including degree of syncarpy, ontogenetic patterns, and PTTT structure, favors a closer phylogenetic proximity between Rutaceae and Simaroubaceae, or Rutaceae and Meliaceae. An apomorphic tendency for the order is that the floral apex is integrated in the syncarpous or apocarpous gynoecium, but with different length and shape among families. Nitrariaceae shares similar stigmatic features and PTTT structure with many Sapindaceae. As the current position of both families in Sapindales is uncertain, floral features should be investigated more extensively in future studies. Two different types of gynophore were identified in the order: either derived from intercalary growth below the gynoecium as a floral internode, or by extension of the base of the ovary locules as part of the gynoecium. Sapindales share a combination of gynoecial characters but variation is mostly caused by different degrees of development of the synascidiate part relative to the symplicate part of carpels, or the latter part is absent. Postgenital fusion of the upper part of the styles leads to a common stigma, while stylar lobes may be separate. Due to a wide variation in these features, a new terminology regarding fusion is proposed to describe the gynoecium of the order.

Keywords Apomorphic tendency · Carpellodes · Congenital fusion · Fruit · Gynoecium architecture · Postgenital fusion · Syncarpy · Vascularization

Introduction

Sapindales are a monophyletic order within the malvid clade of rosids (core eudicots). It comprises nine families—Anacardiaceae, Biebersteiniaceae, Burseraceae, Kirkiaceae, Meliaceae, Nitrariaceae, Rutaceae, Sapindaceae and Simaroubaceae—with 470 genera and 6570 species, mostly distributed in tropical and temperate areas of the world (APG IV 2016; Kubitzki 2011). Sapindalean taxa have diverse floral morphologies and thus represent an interesting group to address questions on comparative floral structure and evolution (*e.g.*, Acevedo-Rodríguez et al. 2011; Engler 1931). A previous comparative study focusing on the evolution of several vegetative and reproductive traits in Sapindales (among others) was based on a limited sample of taxa—nine

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genera of the order (Ronse De Craene and Haston 2006). Also, the study pre-dates the current phylogenetic relationships of Sapindales.

More recently an increasing amount of detailed studies focusing on the comparative morphology, anatomy, histology and ontogeny of flowers of several sapindalean taxa has been carried out (Table 1; *e.g.*, Alves et al. 2017; Avalos et al. 2019; Bachelier and Endress 2008, 2009; Bachelier et al. 2011; Cao et al. 2017, 2018; El Ottra et al. 2013, 2019; Pirani et al. 2010; Ramp 1988; Tölke and Demarco 2020; Wei et al. 2011, 2015). Most of these studies pay special attention to detailed aspects of gynoecium structure. Therefore, this is the right time for a new comparative study synthesizing the knowledge on the Sapindalean gynoecium accumulated so far.

New molecular phylogenetic reconstructions of the Sapindales taxa continuously improve and provide support for current hypotheses on the relationships among its members (Lin et al. 2018; Muellner-Riehl et al. 2016). The monogeneric Biebersteiniaceae is considered the earliest branching lineage of Sapindales, followed by Nitrariaceae (Muellner-Riehl et al. 2016; Stevens 2001 onwards), composed of three genera (*Peganum*, *Nitraria* and *Tetradiclis*). Kirkiaceae is also monogeneric, and forms a sister group with Anacardiaceae plus Burseraceae. These last two families are among the “big six” families of Sapindales (Table 1; Muellner-Riehl et al. 2016). Infraclassical circumscriptions of Anacardiaceae and Burseraceae are still under debate, and herein we follow Pell et al. (2011), for the definition of Anacadioideae and Spondioideae of Anacardiaceae, and Stevens (2001 onwards) for core Burseraceae. Similarly, in Sapindaceae, four subfamilies are currently described (Xanthoceroideae, Hippocastanoideae, Dodonaeoideae, Sapindoideae), but the tribal circumscriptions are still unsettled (Stevens 2001 onwards). The large Rutaceae is currently divided in two subfamilies according to Groppo et al. 2012: the early diverging Cneoroideae, and Rutoideae, which is the most diversified. In alternative classifications, members of the latter subfamily are split into three (Amyridoideae, Aurantioideae and Rutoideae; Morton and Telmer 2014) or six subfamilies (Amyridoideae, Aurantioideae, Haplophylloideae, Rutoideae, Zanthoxyloideae, Cneoroideae; Appelhans et al. 2021). Simaroubaceae is a relatively small family (Table 1) currently formed almost only by members of the former subfamily Simarouboideae of Engler (1931), which included five other subfamilies; four of these have been excluded from Sapindales, while Kirkioidae was raised as Kirkiaceae (Clayton 2011). The Meliaceae is currently divided in two subfamilies: the early diverging Cedreloideae, and Melioideae, which is the most diversified (Koenen et al. 2015; Muellner et al. 2008).

However, some relationships among sapindalean families are not yet well supported, such as: (1) the sister group

relationship between Biebersteiniaceae and eight remaining families; (2) the sister group relationship between Nitrariaceae with all other seven families, except for Biebersteiniaceae; and, (3) the sister group relationship between the clade (Kirkiaceae (Burseraceae, Anacardiaceae)) and (Sapindaceae (Simaroubaceae, Rutaceae, Meliaceae)). Furthermore, the sister relationships of Meliaceae, Simaroubaceae, and Rutaceae is still uncertain. In fact, the relationships among these families have presented conflicting results in recent studies (Gadek et al. 1996; Lin et al. 2018; Magallón et al. 2015; Muellner-Riehl et al. 2016), leading some authors to maintain the three families in a polytomy (Stevens 2001 onwards). Among these three families, Meliaceae is the one with fewest detailed comparative studies on flowers with emphasis on the gynoecium. Gouvêa et al. (2008a, b) studied floral traits of Cedreloideae taxa (Meliaceae), but with limited details on gynoecium ontogeny. In fact, there is a lack of developmental information on the inner morphological surface of carpels in Meliaceae (Bachelier and Endress 2009; Endress 2015). This prevents an accurate comparison of the gynoecium structure of Meliaceae with other Sapindales, especially its most closely related families Rutaceae and Simaroubaceae (Gadek et al. 1996; Lin et al. 2018; Muellner-Riehl et al. 2016; Stevens 2001 onwards), where such studies are available (see Table 1).

In order to fill these gaps, we conducted a review on the gynoecium of Sapindales with emphasis on its morphology, anatomy and ontogeny. We focused on specific features that have either been evaluated before in evolutionary studies but not in the current phylogenetic context of the order (Ronse De Craene and Haston 2006), or that are relevant issues previously discussed in single-family studies (*e.g.* Bachelier and Endress 2009; Bachelier et al. 2011). Also, we analysed features that were compared for the angiosperm gynoecium in general (Endress 2015, 2019) herein compared with a wide focus in Sapindales. While doing an extensive review of the literature (for a full list of the consulted literature see Online Resource 1), we also compared the currently available studies within the current phylogenetic context of sapindalean families (Groppo et al. 2012; Muellner-Riehl et al. 2016; Stevens 2001 onwards). Our aim was to provide a clear picture of the patterns of structural variations found in the gynoecium described in the following eight topics of this review. Additionally, we conducted a detailed study on the structure of the gynoecium of one species of Meliaceae (*Trichilia pallens* C. DC., for details, see material and methods in Online Resource 2), to fill the gap in our knowledge of gynoecium ontogeny in the family and to provide an accurate comparison to the gynoecium structure of other Sapindales. Development of angiospermy is also provided for one Sapindaceae species (*Cardiospermum halicacabum* L., for details, see material and methods in Online Resource 2).

Table 1 General information and references for detailed studies on the gynoecium structure of Sapindales

Family	Number of genera/ number of species ¹	Genera studied	Selected references
Biebersteiniaceae	1/5	<i>Biebersteinia</i>	Boesewinkel (1997), Knuth (1912), Langran and Vassiliades (2008) and Yamamoto et al. (2014)
Nitariaceae	3/13	<i>Nitaria</i> , <i>Peganum</i> , <i>Tetradiclis</i>	Bachelier et al. (2011), Ronse De Craene and Smets (1991) and Ronse De Craene and Haston (2006)
Kirkiaceae	1/8	<i>Kirkia</i>	Bachelier and Endress (2008) and Ramp (1988)
Anacardiaceae	80/873	<i>Amphipterygium</i> , <i>Anacardium</i> , <i>Blepharocarya</i> , <i>Buchanania</i> , <i>Campnosperma</i> , <i>Dobinea</i> , <i>Dracontomelon</i> , <i>Gluta</i> , <i>Harpephyllum</i> , <i>Loxopteridium</i> , <i>Loxostylis</i> , <i>Mangifera</i> , <i>Mycronychia</i> , <i>Pentaspadon</i> , <i>Pistacia</i> , <i>Pleioygnium</i> , <i>Pseudospondias</i> , <i>Rhus</i> , <i>Rhodosphaera</i> , <i>Schinopsis</i> , <i>Schinus</i> , <i>Semeacarpus</i> , <i>Solenocarpus</i> , <i>Smodingium</i> , <i>Spondias</i> , <i>Tapiritira</i>	Bachelier and Endress (2007, 2009), Gonzalez (2016), Tavares et al. (2020), Tölke and Demarco (2020), Tölke et al. (2021) and Wannan and Quinn (1991)
Burseraceae	19/775	<i>Beiselia</i> , <i>Boswellia</i> , <i>Bursera</i> , <i>Canarium</i> , <i>Commiphora</i> , <i>Garuga</i> , <i>Pentaspadon</i> , <i>Protium</i> , <i>Santiria</i>	Bachelier and Endress (2009) and Narayana (1960a, b)
Sapindaceae	144/1,925	<i>Acer</i> , <i>Averrhoidium</i> , <i>Cardiospermum</i> , <i>Delavaya</i> , <i>Dimocarpus</i> , <i>Dodonea</i> , <i>Eurycorymbus</i> , <i>Handeliidendron</i> , <i>Koelreuteria</i> , <i>Lichi</i> , <i>Paullinia</i> , <i>Serjanita</i> , <i>Urvillea</i> , <i>Xanthoceras</i>	Avalos et al. (2019), Cao and Xia (2009), Cao et al. (2006, 2017, 2018), Paoli and Sarti (2008), Peck and Lersten (1991a, b), Ronse De Craene et al. (2000), Weckerte and Rutishauser (2003, 2005), Zhou et al. (2019) and Xu (1990, 1991)
Meliaceae	50/641	<i>Aglaiia</i> , <i>Aphanamixis</i> , <i>Azadirachta</i> , <i>Cedrela</i> , <i>Chukrassia</i> , <i>Dysoxylum</i> , <i>Guarea</i> , <i>Hynaea</i> , <i>Melia</i> , <i>Soymida</i> , <i>Toona</i> , <i>Swietenia</i> , <i>Trichilia</i> , <i>Toona</i> , <i>Turrea</i> , <i>Walsura</i>	Gama et al. (2021a, b), Gouvêa et al. (2008a, b), Lal (1994), Murty and Gupta (1978a, b), Nair (1958, 1959a, b, 1962, 1963), Nair and Kanta (1961), Narayana (1958, 1959) and Souza et al. (2001, 2002)
Simaroubaceae	19–22/110	<i>Ailanthus</i> , <i>Brucea</i> , <i>Homalolepis</i> , <i>Leimera</i> , <i>Quassia</i> , <i>Samadera</i> , <i>Simaba</i> , <i>Simarouba</i> , <i>Soulamea</i>	Abbe and Earle (1940), Alves et al. (2017), Endress et al. (1983), Nair and Joseph (1957), Nair and Joshi (1958), Nair and Sukumaran (1960), Narayana and Sayeeduddin (1958) and Ramp (1988)
Rutaceae	161/2085	<i>Adiscanthus</i> , <i>Agasthoma</i> , <i>Angostura</i> , <i>Boeninghausenia</i> , <i>Boronella</i> , <i>Boronia</i> , <i>Calodendrum</i> , <i>Choisya</i> , <i>Citrus</i> , <i>Clausena</i> , <i>Cneorum</i> , <i>Coleonema</i> , <i>Conchocarpus</i> , <i>Correa</i> , <i>Dictamnus</i> , <i>Dryades</i> , <i>Eriostemon</i> , <i>Erythrochiton</i> , <i>Ertela</i> , <i>Galipea</i> , <i>Haplophyllum</i> , <i>Harrisonia</i> , <i>Horatia</i> , <i>Metrodorea</i> , <i>Murraya</i> , <i>Phellodendron</i> , <i>Pilocarpus</i> , <i>Prelea</i> , <i>Raputiarana</i> , <i>Rautia</i> , <i>Ravenia</i> , <i>Rutta</i> , <i>Sigmathanthus</i> , <i>Skimmia</i> , <i>Tetradium</i> , <i>Zanthoxylum</i> , <i>Zeria</i>	Beurton (1994), Caris et al. (2006), El Ottra et al. (2013, 2019), Endress et al. (1983), Gut (1966), Hartl (1957), Lord and Eckard (1985), Moore (1936), Prani et al. (2010), Ramp (1988), Sheelal and Narayana (1994), Souza et al. (2003, 2004), Tiliak and Nene (1978), Tilson and Bamford (1938), Wei et al. (2011, 2015) and Yamazaki (1988)

¹The number of genera and species are based on Stevens (2001 onwards)

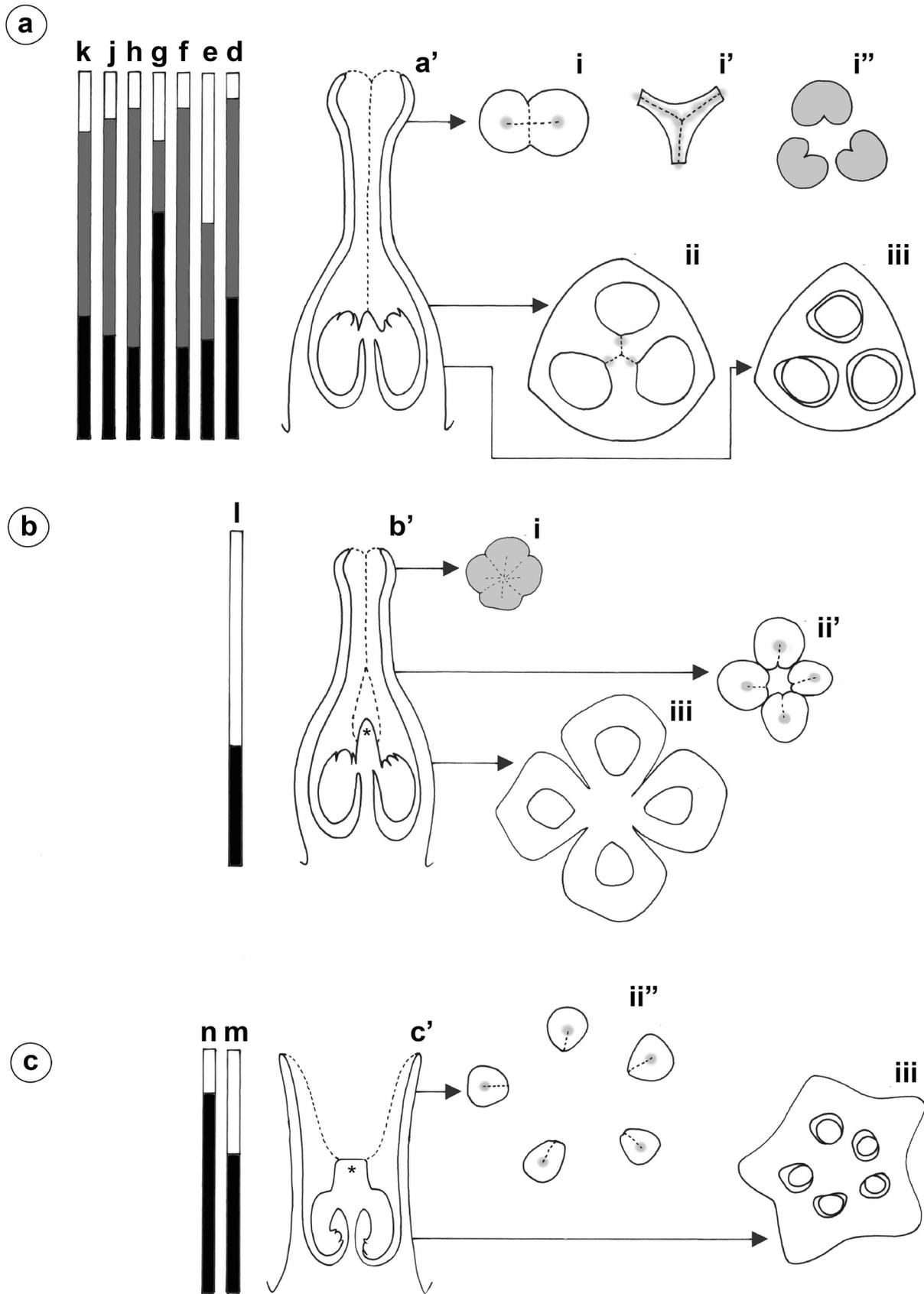


Fig. 1 Summary of the syncarpous gynoecium structure in Sapindales. Schematic median longitudinal section (a', b', c'), schematic transections (i, i', i'', ii, ii', ii'', iii); examples of variations in the extent of each zone of the syncarpous gynoecium are indicated by the bars on the left of the longitudinal section (d–h, j–n; white bars=apocarpous zone; dark grey bars=syncarpous, symplicate zone; black bars=syncarpous, synascidiate zone). Postgenitally fused areas are indicated by hatched lines; pollen tube transmitting tract, light grey; i postgenitally fused stylar lobes, plicate; i' postgenitally fused stylar lobes apparently unifacial in Nitrariaceae; i'' separate stylar lobes, asympligate; ii symplicate zone; ii' apocarpous zone at the style, plicate, and in ii'' widely separate throughout its length; iii synascidiate zone. a Most common type in the order, with the three zones usually found in syncarpous gynoecia, such as in *Trichilia* (Meliaceae, d), syncarpous Rutoideae and *Averhoidium* (e; f only found in Aurantiaceae), *Beiselia* (Burseraceae, g), *Protium* (core Burseraceae, h), Paullinieae (Sapindaceae, j), and *Nitraria* (Nitrariaceae, k). b and c Less common types of syncarpous gynoecia, without a symplicate zone. b In *Kirkia* (Kirkiaceae) and *Dracontomelon* (Anacardiaceae); ii' ascidiate in *Dracontomelon* and plicate in *Kirkia* the style is postgenitally fused for most of its length, while in c style is widely separate, such as found in *Spondias* (m), *Pleiogynum* (n), and other Anacardiaceae (modified from Bachelier and Endress (2009); i' modified from Bachelier et al. (2011) and b modified from Bachelier and Endress (2008)). Asterisks: floral apex, indicated only in longitudinal schemes

Structural studies are important as a concatenation to the information coming from molecular phylogenetic studies to build adequately hypotheses on the evolutionary history of plants (Endress and Matthews 2012; Tobe 2003). In this context, we additionally aim to provide detailed characters of the gynoecium that potentially support problematic systematic relationships among families of Sapindales. In this review we found new features that are considered “apomorphic tendencies” (Endress 2003, 2010; Endress and Matthews 2012), which highlights the importance of the presence of common traits within clades. Though not strictly synapomorphic, finding such traits is important as they set new directions for future evo-devo integrative studies where similar developmental pathways may be found to be shared in a same clade (Endress and Matthews 2012; Ronse De Craene 2018), and variations found within a clade could be explained by “similar developmental constraints” (Ronse De Craene 2018).

Syncarpous versus apocarpous zones of the gynoecium

For the definition of the syncarpous and apocarpous zones of the gynoecium, considering the inner morphological surfaces of carpels and their intercarpellary union, we herein follow Leinfellner (1950). Leinfellner defines the syncarpous zone of the gynoecium as the region with carpels congenitally fused at their flanks and centre (*i.e.*, synascidiate zone), or only at their flanks in variable degrees (*i.e.*, symplicate

zone/hemisymphlicate zone). All other regions of the gynoecium are defined as the apocarpous zone, including carpels completely free or postgenitally fused in variable degrees, but without intercarpellary congenital fusion (Leinfellner 1950). There is a large variation in these zones among Sapindales, and as a consequence, gynoecia are frequently described as “mostly syncarpous” or “mostly apocarpous”, depending on which of these zones is predominant (Figs. 1 and 2), as described further in this topic. For *Bieberstenia*, Biebersteiniaceae, there are few detailed studies on gynoecium morphology. Still, some general conclusions can be drawn from morphological and embryological studies (Table 1). The five carpels appear syncarpous in the lower half of the ovary, completely apocarpous (free) above, and postgenitally united distally forming a single style in young stages of gynoecium development (Yamamoto et al. 2014; see there Figs. 2b, c and 3c). A postgenitally fused stigmatic head, as described for other Sapindales (*e.g.* Bachelier and Endress 2008), is likely present in the anthetic gynoecium, as it is described as “capitate” (Knuth 1912). However, the proportions among the syncarpous and apocarpous zones likely change in the anthetic gynoecium, since Knuth (1912) and Langran and Vassiliades (2008) describe the gynoecium composed of five free carpels, and fruits as schizocarp with five mericarps. Considering their descriptions, the gynoecium in Biebersteiniaceae would fit the gynoecium structure already described for other Sapindales as apocarpous (see below; Table 2). However, further ontogenetic studies of the inner and outer morphological surfaces of carpels in *Biebersteinia* are needed to supplement the study of Yamamoto et al. (2014).

There are detailed studies available for Nitrariaceae (Table 1). *Peganum* is mostly syncarpous, apocarpous but postgenitally fused from the mid-level of the style to the stigma (Ronse De Craene et al. 1996). *Nitraria* has a shorter apocarpous and symplicate zone than *Peganum*: it is syncarpous up to the style and apocarpous only in its distal part (Ronse De Craene and Smets 1991; Table 2, Fig. 1a, a', k, i', ii, iii). For *Tetradiclis* details on the inner morphological surfaces of carpels are limited (Bachelier et al. 2011). In Nitrariaceae there is a large variation in the respective length of these zones comprising the syncarpous (synascidiate/symplicate) or apocarpous (plicate/asympligate) part of the gynoecium (Table 2). Due to its position in the phylogeny of Sapindales, we can infer that alterations in the proportion of the apocarpous and syncarpous zones of the gynoecium are labile features present from the early stages of diversification of the order.

Kirkiaceae is unusual in having no symplicate zone in the ovary, which is a feature also shared with some multicarpellate Spondioideae of Anacardiaceae (Table 2; Bachelier and Endress 2008; Ramp 1988). Instead the ovary is entirely synascidiate, up to half the length of the style, where it is

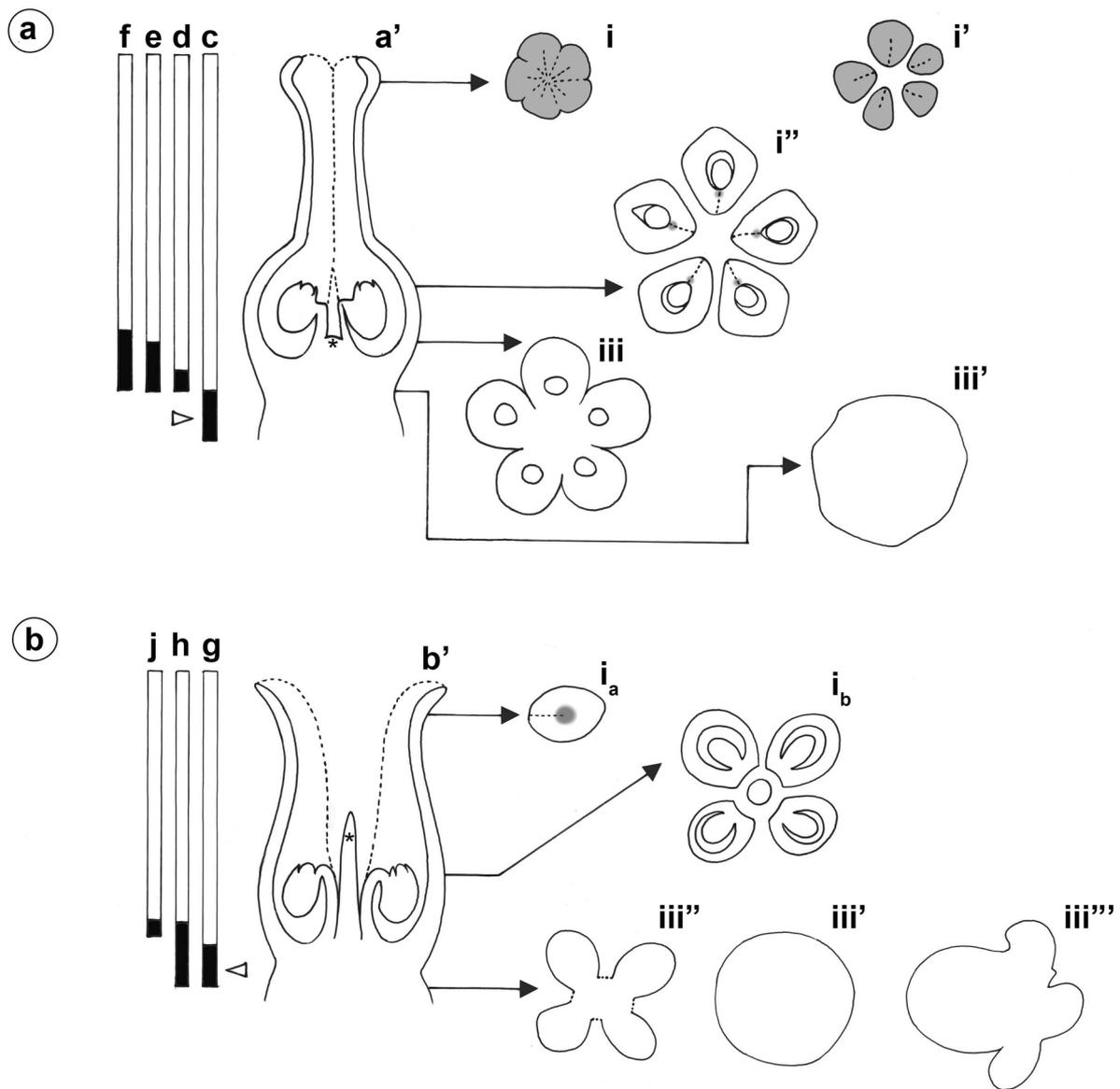


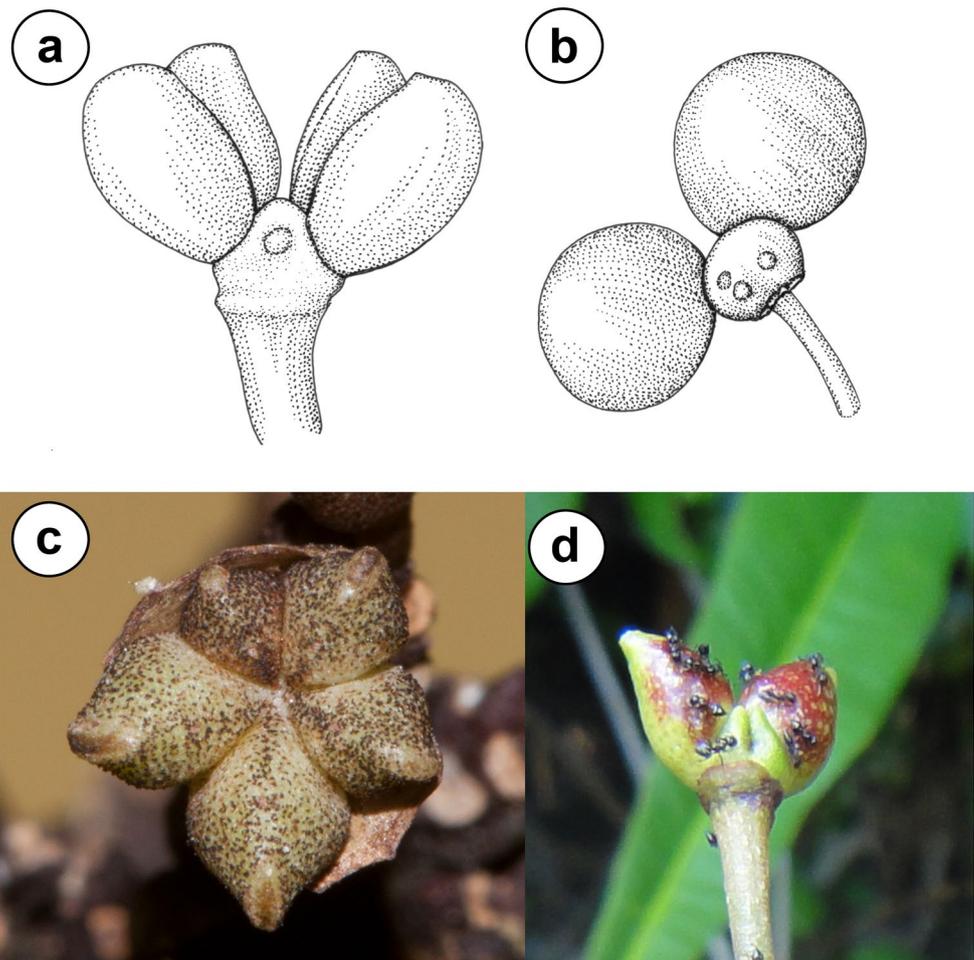
Fig. 2 Summary of apocarpous gynoecium structure in Sapindales. Schematic median longitudinal section (**a'**, **b'**), schematic transections (**i**, **iii**, **i'**, **i''**, **iii'**, **iii''**, **iii'''**, **i_a**, **i_b**); examples of variations in the extent of each zone of the gynoecium are indicated at the bars at the left side of the longitudinal section (**c–h**, **j**; white bars = apocarpous zone; black bars = syncarpous, synascidiate zone; white arrowhead, region of the gynophore). Note that there is no symplicate zone. Postgenitally fused areas are indicated by hatched lines; pollen tube transmitting tract, light grey; **i** postgenitally fused stylar lobes, plicate; **i'** separate stylar lobes, plicate; **i''** plicate and free carpel at the ovary level; **i_a** plicate carpels, with styles separate throughout their length; only one carpel represented; **i_b** ascidiate carpels at the ovary level with floral apex at centre; **iii**, **iii'**, **iii''**, **iii'''** short synascidiate zone, at the base of the locules (**iii**), below the locules (**iii'**) and/or at the

level of the gynophore (**iii'**, **iii''**). **a** Apocarpous gynoecium with postgenitally united styles, found in Simaroubaceae and Rutaceae, such as *Ailanthus* (**c**), *Simaba* (**d**), and apocarpous Rutoideae (e.g., *Conchocarpus* spp., **e** and *Adiscanthus*, **f**). **b** Apocarpous gynoecium with separate styles, found in Simaroubaceae (*Brucea*, **g**, with floral apex uplifted to the ovary apex, as depicted in the longisection and in **i_b**; with lobed gynophore, **iii''**), Rutaceae (*Zanthoxylum*, **h**, floral apex not uplifted, and entire gynophore, **iii'**) and pseudomonomerous Anacardiaceae (*Buchanania* **j**, floral apex not uplifted, and only one carpel develops a locule; without gynophore, **iii'''**). **i_a**, **iii'** modified from Ramp (1988); **i_b**, **iii''** from Nair and Joshi (1958); **iii'''** from Bachelier and Endress (2009). Asterisks: floral apex, indicated only in longitudinal schemes

postgenitally fused, distally forming a single style and a stigmatic head (Tables 2 and 3). The floral apex is conspicuous at the centre of the synascidiate zone (Fig. 1b, **i**, **i'**,

iii). Although carpels are centrally fused in the synascidiate zone, it is noteworthy that a large extent of the lateral flanks of each carpel bulges out (Fig. 1b, **iii**), giving the misleading

Fig. 3 Morphology of young fruiting carpels from Simaroubaeae (a, b) and Rutaceae (c, d, photographs); style already dropped off. Note the fruitlets widely separate. **a** *Simarouba* and *Picrasma* (b), united only by the conspicuous gynophore. **c** *Conchocarpus* and *Adiscanthus* (d), but without conspicuous gynophore in fruit stage, fruitlets united only by their base. Modified from Pirani 1987 (a) and Devecchi and Pirani 2020 (b). Photographs, J.H.L.El Ottra



impression of apocarp, from a superficial inspection of the outer surface of the ovary (Bachelier and Endress 2008; Ramp 1988). Probably due to this large expansion of the lateral flanks of the ovary, weakness zones are created for a later separation of the fruitlets. In fact, the fruiting carpels separate at maturity, forming a “schizocarp”, with “mericarps pendulous from a columella” (Stevens 2001 onwards).

For the Burseraceae and Anacardiaceae clade (Muellner-Riehl et al. 2016) extensive information is available on fusions and on the extent of the carpellary zones (Bachelier and Endress 2007, 2009; Wannan and Quinn 1991). Similar to the Kirkiaceae, an “extensive synascidiate” zone is found; Fig. 1b, c, iii; Table 2). This is a putative synapomorphy for these three families (Bachelier and Endress 2009). Though there is a wide variation in the proportion between different carpellary zones, some general patterns were found. The Burseraceae gynoecium is considered to have more “plesiomorphies” in its features compared to other Sapindales, such as Anacardiaceae (Bachelier and Endress 2009). In tribe Beiselieae (*Beiselia*) of Burseraceae, a long synascidiate zone occurs comprising the largest part of the gynoecium—as the stigma is sessile, a distinct style is not

discernable (Table 2; Fig. 1a, g, i). In contrast, “core Burseraceae” (tribes Garugeae, Bursereae and Protieae) share a long symplicate zone as a putative apomorphy (Table 2; Fig. 1a, h; Stevens 2001 onwards). In general, Burseraceae present postgenital fusion of carpel tips, forming a stigmatic head. In *Canarium* a stigmatic head can also be formed by “contiguity” of carpels only, “without fusion”. Contiguity of stigmatic tips is also found among Anacardiaceae–Spondioidae (Bachelier and Endress 2009; Pell et al. 2011).

In Anacardiaceae more complex forms of gynoecium architecture are found as compared to Burseraceae, which is reflected also in a wider variation in the proportion of each carpellary zone. In multicarpellate taxa of Spondioidae there is no symplicate zone of the ovary, similar to Kirkiaceae, and carpels are synascidiate for the entire ovary in most taxa (except *Buchanania*), directly shifting to the apocarpous (plicate) zone (Fig. 1c, m, n, ii”, iii; Table 2; Bachelier and Endress 2007, 2009; Wannan and Quinn 1991). Carpels at this level (*i.e.*, the style and stigma) can be free and separated (*Spondias purpurea* L., *S. tuberosa* Arruda, *Buchanania*, *Pleiogynum*; *Tapirira guianensis* Aubl.; Fig. 1c, ii”) or only contiguous (*Spondias dulcis*

Table 2 Type of gynoecium* and relative length of the syncarpous and apocarpous zones in multicarpellate gynoecia of Sapindales

Family	Genus or infrafamiliar group	Type of gynoecium*	Syncarpous zone	Apocarpous zone
Biebersteiniaceae	<i>Biebersteinia</i>	Apocarpous (?)	–	–
Nitriaceae	<i>Peganum</i>	Syncarpous	Synascidiate in the lower half of the ovary; symplicate up to mid-level of the stigma	Mid-level of the style up to the stigma
	<i>Nitraria</i>	Syncarpous	Long synascidiate zone, comprising most of the ovary, symplicate above up to the distal part of the style	Distal part of the style up to the stigma
	<i>Tetradiclis</i>	Syncarpous (?)	Shortly synascidiate and symplicate at base of the ovary	Entire style and stigma (?)
Kirkiaceae	<i>Kirkia</i>	Syncarpous	Long synascidiate zone, comprising the entire ovary (symplicate zone absent)	Entire style and stigma
Anacardiaceae	Multicarpellate Spondioideae	Syncarpous	Long synascidiate zone, comprising the entire ovary at least (symplicate zone absent)	Style (variable levels) and stigma
	<i>Buchanania</i>	Apocarpous	Short synascidiate zone in the base of the ovary (symplicate zone absent)	Most part of the ovary, style and stigma
Burseraceae	Beiseliace (<i>Beiselia</i>)	Syncarpous	Long synascidiate zone, comprising the entire ovary; symplicate only in the transition level to the stigma	Stigma (style absent)
	Core Burseraceae	Syncarpous	Long symplicate zone, comprising part of the ovary and style; synascidiate up to mid-level of the ovary	Distal part of the style up to the stigma
Sapindaceae	Xanthoceroatoideae	Syncarpous (?)	–	–
	Dodonaeoideae (<i>Eurycorymbus</i> and <i>Averrhoidium</i>)	Syncarpous	Synascidiate up to the lower half of the ovary, symplicate up to the base of the style (only for <i>Averrhoidium</i>)	Style (variable levels) and stigma (for <i>Averrhoidium</i>); distal part of the style and stigma (?) in <i>Eurycorymbus</i>
	Hippocastanoideae (<i>Acer</i> , <i>Handeliidendron</i>)	Syncarpous	Synascidiate up to mid-level (?) of the ovary, symplicate above (only for <i>Acer</i>)	Entire style and stigma (<i>Acer</i>); distal part of the style and stigma (?) in <i>Handeliidendron</i>
	Sapindoideae (Paullinieae)	Syncarpous	Synascidiate up to the distal part of the ovary, symplicate above and at the style level	Stigma (?)
	Sapindoideae (<i>Koelreuteria</i>)	Syncarpous	Synascidiate up to the upper half of the ovary, symplicate above in variables levels (?) and up to the style	Stigma
Simaroubaceae	Most taxa, except <i>Soulamea</i> (?)	Apocarpous	Short synascidiate zone in the gynophore and/or at the base of the ovary (symplicate zone absent)	Most part of the ovary, style and stigma
Rutaceae	Cneoroideae	Syncarpous/apocarpous (<i>Dyctioloma</i> ?)	Synascidiate up to the lower third of the ovary, symplicate above (only for <i>Harrisonia</i>)	Style and stigma (only for <i>Harrisonia</i>)
	Rutoideae (<i>Boeninghausenia</i> , <i>Boronella</i> , <i>Correa</i> , <i>Eriostemon</i> , <i>Pilocarpus</i> , <i>Tetradium</i> , <i>Zanthoxylum</i> , <i>Zieria</i> , and subtribe Galipeinae)	Apocarpous	Short synascidiate zone in the gynophore and/or at the base of the ovary (in the lower half of the ovary, at different levels; symplicate zone absent)	Most part of the ovary, style and stigma

Table 2 (continued)

Family	Genus or infrafamilial group	Type of gynoecium*	Syncarpous zone	Apocarpous zone
	Rutoideae (<i>Calodendrum</i> , <i>Coleonema</i> , <i>Ruta</i> , <i>Prelea</i> , <i>Skimmia</i> , <i>Phellodendron</i>)	Syncarpous	Synascidiate zone half the length of the ovary (rarely less, in <i>Coleonema</i> , or in most of the ovary length in <i>Skimmia</i>); symplicate zone above, and up to the base of the style	Most part of the style and stigma
	Rutoideae tribe Aurantieae**	Syncarpous	Synascidiate in the lower half of the ovary and symplicate above, up to uppermost level of the style	Stigma
Meliaceae	Cedreloideae	Syncarpous (?)	Symplicate zone in the upper part of the ovary (?)	Distal part of the style and stigma (?)
	Melioidae— <i>Trichillia</i>	Syncarpous	Synascidiate in the lower two thirds of the ovary, symplicate above and up to the distal part of the stigma	At the very tip of the stigma
	Other Melioidae	Syncarpous (?)	Symplicate zone in the upper part of the ovary (?)	–

*Type of gynoecium defined according to our terminology of apocarpous or syncarpous as proposed in topic 3 (see text)

**Aurantioideae of Appelhans et al. (2021)

–No available data

(?) Further detailed studies are necessary to corroborate our impressions from studies with incomplete ontogenetic series/cross section series

Table 3 Synthesis of main patterns of variations in gynoecial features of Sapindales

Family	Stigmatic head: presence vs absence	PTTT type	Floral apex: presence vs absence	Shape/relative degree of exposure of the floral apex	Style position	Early carpel ontogeny
Biebersteiniaceae	Present (?)	–	Present	Convex/enclosed in the ovary (?)	Basistylous	–
Nitriaceae	Present (<i>Tetradiclis</i> only, by fusion)	Closed and open*	Absent	N.A	Basistylous/slightly anacrostylous/acrostylous	Carpels arise as separate Primordia of variable form
Kirkiaceae	Present (by fusion)	Closed and open*	Present	Rounded (convex)/not enclosed in the ovary, covered by carpel tips	Acrostylous	Carpels arise as separate reniform primordia
Anacardiaceae	Absent, rarely present, by fusion or contiguity (in Spondioideae)	Closed and open*/open	Present	Convex/not enclosed in the ovary, covered by carpel tips, or not (exposed)	Strongly anacrostylous**/acrostylous	Variable patterns
Burseraceae	Present (either by fusion or contiguity)	Closed and open (?)*	Present	Convex/enclosed in the ovary (except <i>Beiselia</i>)	Acrostylous	–
Sapindaceae	Present (?) in <i>Averrhoidium dalyi</i>	Open or half-closed	Absent	N.A	Basistylous/strongly anacrostylous/acrostylous	Carpels arise in a triangular meristem***
Meliaceae	Present (by fusion)	Open	–	–	Acrostylous	Carpels arise in a triangular meristem (only in <i>Trichilita</i>)
Simaroubaeaceae	Absent or present (by fusion)	Closed	Present	Rounded or conical/enclosed in the ovary (except in <i>Brucea</i>)	Slightly to strongly anacrostylous	Ovary arise first as reniform primordia
Rutaceae	Absent or present (by fusion)	Closed (most Rutoideae, except Aurantieae); open (<i>Harrisonia</i> and <i>Aurantieae</i>)	Present	Flat or convex/enclosed in the ovary	Basistylous/slightly to strongly anacrostylous	Ovary arise first as reniform primordia (apocarpous Rutoideae); variable patterns in syncarpous taxa

Table 3 (continued)

Family	Stigmatic features	Patterns of vascularization in the dorsal region of the ovary ¹	Patterns of vascularization in the ventral region of the ovary ¹	Patterns of vascularization at the level of the style ¹	Stalk-like elongations of the axis
Biebersteiniaceae	–	–	–	–	Gynophore
Nitriaceae	Commissural stigmas	Diffuse dorsal vasculature	Synlaterals/two free ventral bundles	Dorsal bands of vascular tissue	Gynophore
Kirkiaceae	Uniseriate multicellular trichomes	Diffuse dorsal vasculature	Synlateral bundles	Two free ventral bundles	Gynophore
Anacardiaceae	Uniseriate multicellular trichomes	Diffuse dorsal vasculature ⁴ (many taxa) /one main median dorsal bundle (<i>Spondias</i> ⁵)	Two free ventral bundles (<i>Blerocaryca</i> ⁸ , <i>Rhus</i> ⁸ ; <i>Anacardium</i> ⁹)	Two free ventral bundles (<i>Dobinea</i> ⁸ , <i>Schinus</i> ^{8,4} , <i>Anacardium</i> ^{2,9} , <i>Rhus</i> ^{2,8} , <i>Rhodospaera</i> ^{2,8}) dorsal bundles only (<i>Anacardium</i> ¹⁰ , <i>Blerocaryca</i> ⁸ , <i>Pleiogynum</i> ⁴ , <i>Spondias</i> ⁴ and <i>Tapirira</i> ¹) one dorsal plus two ventrals (<i>Dracontomelon</i> ⁸ , <i>Mangifera</i> ⁸ , <i>Schinopsis</i> ¹² , <i>Rhodospaera</i> ^{3,8} , <i>Amphipteridium</i> ¹³)	Gynophore
Bursaceae	Uniseriate multicellular trichomes	One (or two) main median dorsal bundle(s) (<i>Garriga</i> ⁶)/diffuse dorsal vasculature (<i>Bursera</i> ⁷ , <i>Boswellia</i> ⁶)	Synlateral bundles (<i>Bursera</i> ⁷ , <i>Boswellia</i> ⁶ , <i>Garuga</i> ⁶)	Two free ventral bundles (<i>Boswellia</i> ⁶ , <i>Santiria</i> ⁴) dorsal bundles only (<i>Beiselia</i> ⁴)	Androgynophore
Sapindaceae	Commissural stigmas. Twisted, screw-like in <i>Averrhoidium</i> ⁴ . Smooth (rare) Free branches in <i>Acer</i> ^{15,16} , <i>Licht</i> ¹⁷ , <i>Dinocarpus</i> ¹⁷ , <i>Cardiospermum</i> ¹⁸ , <i>Serjania</i> ¹⁸ , <i>Urvillea</i> ¹⁸ , <i>Paullinia</i> ^{18,19}	One main median dorsal bundle (<i>Dodonaea</i> ²⁰ , <i>Averrhoidium</i> ¹⁴ , many <i>Paullinieae</i> ¹⁸)/diffuse dorsal vasculature (<i>Koelreuteria</i> ^{21,22,23} , <i>Acer</i> ²³ , <i>Aesculus</i> ²³)	Synlateral bundles (many <i>Paullinieae</i> ¹⁸) /two free ventrals (<i>Acer</i> ²³ , <i>Aesculus</i> ²³ , <i>Averrhoidium</i> ¹⁴ , <i>Serjania</i> ¹⁸)	Two free ventrals (<i>Acer</i> ¹⁵ , <i>Aesculus</i> ²³ , <i>Koelreuteria</i> ^{21,22,23}) /single (fused) ventral (<i>Averrhoidium</i> ¹⁴)	Gynophore/androgynophore
Meliaceae	Long unicellular trichomes/ bicellular trichomes/long and short stigmatic cells	One (or two) main median dorsal bundle(s) (<i>Aphanamixis</i> ²⁴ , <i>Cedrela</i> ²⁵ , <i>Swietenia</i> ²⁴ , <i>Chukassia</i> ²⁶ , <i>Azadirachta</i> ²⁶ , <i>Toona</i> ²⁷ , <i>Dysoxylum</i> ²⁴ , <i>Sandoricum</i> ²⁸ , <i>Cipadessa</i> ²⁸ , <i>Trichilia</i> ²⁹) /diffuse dorsal vasculature (<i>Melia</i> ²⁶ , <i>Carapa</i> ²⁸ , <i>Guarea</i> ³⁰) dorsals absent in <i>Soymida</i> ²⁴ , <i>Hynea</i> ³ and <i>Walsura</i> ³¹	Single (fused) ventral (<i>Swietenia</i> ²⁷) /synlaterals (<i>Melia</i> ²⁶ , <i>Cedrela</i> ²⁵ , <i>Soymida</i> ²⁴ , <i>Azadirachta</i> ²⁶ , <i>Aphanamixis</i> ²⁴ , <i>Chukassia</i> ²⁶ , <i>Dysoxylum</i> ²⁴ , <i>Toona</i> ²⁸ , <i>Heynea</i> ³¹ , <i>Walsura</i> ³¹ , <i>Trichilia</i> ²⁹)	Synlaterals (<i>Cedrela huberi</i> <i>Ducke</i> ²⁵ , <i>Soymida</i> ²⁴ , <i>Trichilia</i> ²⁹) one dorsal and two ventrals (<i>Cedrela</i> ²⁵) /two free ventrals (<i>Swietenia</i> ^{26,27,32} , <i>Toona</i> ²⁸ , <i>Naregamia</i> ²⁸ , <i>Hynea</i> ^{24,31} , <i>Walsura</i> ²⁵)	Gynophore/androgynophore
Simaroubaceae	Papillose and smooth stigmas	One (or two) main median dorsal bundle (<i>Homalolepis</i> ³³ , <i>Samadera</i> ³⁴ , <i>Brucea</i> ³⁵) /diffuse dorsal vasculature (<i>Ailanthus</i> ³⁶ , <i>Quassia</i> ³⁶)	Single (fused) ventrals (<i>Leitneria</i> ³⁷ , <i>Samadera</i> ³⁴ , <i>Homalolepis</i> ³³) /two free ventrals (<i>Ailanthus</i> ³⁶ , <i>Quassia</i> ³⁶ , <i>Brucea</i> ³⁵)	Two free ventrals (<i>Ailanthus</i> ³⁶) / one fused ventral (<i>Brucea</i> ³⁵ , <i>Quassia</i> ³⁶) / dorsal bundles (<i>Homalolepis</i> ³³) one dorsal plus two ventrals (<i>Leitneria</i> ³⁷)	Gynophore/androgynophore

Table 3 (continued)

Family	Stigmatic features	Patterns of vascularization in the dorsal region of the ovary ¹	Patterns of vascularization in the ventral region of the ovary ¹	Patterns of vascularization at the level of the style ¹	Stalk-like elongations of the axis
Rutaceae	Papillose and smooth stigmas	One (or two) main median dorsal bundle(s) (<i>Ruta</i> ^{36,38} , <i>Lavanga</i> ³⁸ , <i>Aegle</i> ³⁸ , <i>Atalantia</i> ³⁸ , <i>Citrus</i> ^{36,38} , <i>Murraya</i> ^{36,38} , <i>Harrisonia</i> ³⁶ , <i>Ertela</i> ³⁹ , <i>Raputiarana</i> ³⁹ , <i>Conchocarpus</i> ³⁹ , <i>Sigmatanthus</i> ³⁹ ; in <i>Coleonema</i> only in the anthetic gynoecium ⁴⁰)/diffuse dorsal vasculature (<i>Zanthoxylum</i> ^{36,40} , <i>Terradium</i> ^{36,40} , <i>Choisya</i> ^{36,40} , <i>Boemighausenia</i> ³⁶ , <i>Dictamnus</i> ^{36,40} , <i>Skimmia</i> ³⁶ , <i>Pilocarpus</i> ^{36,40} , many Galipeinae ^{39,41})	Single (fused) ventrals (<i>Aegles</i> ³⁸ , <i>Atalantia</i> ³⁸)/two free ventrals (<i>Ruta</i> ^{36,38} , <i>Terradium</i> ^{36,40} , <i>Choisya</i> ^{36,40} , <i>Boemighausenia</i> ³⁶ , <i>Dictamnus</i> ³⁶ , <i>Eriostemon</i> ³⁶ , <i>Pilocarpus</i> ^{36,40} , <i>Skimmia</i> ³⁶ , <i>Harrisonia</i> ³⁶ , most Galipeinae ³⁹)/synlateras (<i>Chiloxylon</i> ²⁸ , and Aurantiaceae such as <i>Murraya</i> ^{36,38} , <i>Citrus</i> ^{36,38} , <i>Glycosmis</i> ^{36,38} , <i>Fortunella</i> ³⁶ and <i>Feronia</i> ³⁵)	Two free ventrals (<i>Harrisonia</i> ³⁶ , <i>Skimmia</i> ³⁶ , <i>Ptelea</i> ^{36,40} , <i>Phellodendron</i> ³⁶ , <i>Calodendrum</i> ³⁶ , <i>Ruta</i> ^{36,38} , <i>Terradium</i> ^{36,40} , <i>Murraya</i> ^{36,38}), one fused ventral bundle (<i>Eriostemon</i> ³⁶ and most Galipeinae ^{36,39}) synlaterals (<i>Fortunella</i> ³⁶), one dorsal plus two ventrals (Aurantiaceae— <i>Merrilia</i> ⁴² , <i>Wenzelia</i> ⁴² , <i>Lavanga</i> ⁴² , <i>Triphasia</i> ⁴² , <i>Fortunella</i> ^{36,42} , <i>Microcitrus</i> ⁴² , <i>Afraegle</i> ⁴²)	Gynophore/androgynophore

*In a same gynoecium

**Ventrally bulging only in pseudomonomerous taxa of Anacardiaceae

***In most taxa, with trimerous gynoecium

¹ Considering each carpel

² Only in carpelodes

³ Only in fertile carpels

⁴ Bachelier and Endress (2009)

⁵ Tölke et al. (2021)

⁶ Narayana (1960a)

⁷ Narayana (1960b)

⁸ Wannan and Quinn (1991)

⁹ Ronse De Craene and Haston (2006)

¹⁰ Tölke and Demarco (2020)

¹¹ Tölke et al. (2021)

¹² Gonzalez (2016)

¹³ Bachelier and Endress (2007)

¹⁴ Weckerle and Rutshauser (2003)

¹⁵ Peck and Lersten (1991a)

¹⁶ Yadav et al. (2016)

¹⁷ Xu (1990, 1991)

¹⁸ Weckerle and Rutshauser (2005)

¹⁹ Solís et al. (2017)

²⁰ Paoli and Sarti (2008)

²¹ Avalos et al. (2019)

Table 3 (continued)

- ²²Ronse De Craene et al. (2000)
²³Ronse De Craene and Hasston (2006)
²⁴Murty and Gupta (1978a)
²⁵Lal (1994)
²⁶Murty and Gupta (1978b)
²⁷Narayana (1958)
²⁸Nair (1963)
²⁹This study
³⁰Souza et al. (2002)
³¹Narayana (1959)
³²Nair (1962)
³³Alves et al. (2017)
³⁴Nair and Joseph (1957)
³⁵Nair and Joshi (1958)

Forst., *Spondias macrocarpa* Engl.), or more rarely proximally free and distally postgenitally fused (*Dracontomelon*; Fig. 1b, b', l), forming a stigmatic head (Fig. 1b, i). *Buchanania* differs from the above taxa by its mostly apocarpous gynoecium. The apocarpous zone comprises not only the style but most part of the ovary as well. It has only a very short synascidiate base, with three of the four carpels sterilized (Fig. 2a, b, j, iii'''). In fact, in many Anacardiaceae different degrees in reduction of carpels lead to a lower gynoecial merism and to the formation of a monomerous or pseudomonomerous gynoecium. These two types can in some cases be difficult to differentiate as the result of a gradual shift, but are considered an autapomorphy of Anacardiaceae (Bachelier and Endress 2009), more frequently found in Anacardioideae (Bachelier and Endress 2007, 2009; Copeland 1961; Gonzalez 2016; Tölke and Demarco 2020; Tölke et al. 2021; Wannan and Quinn 1991). Due to this dubious interpretation that causes difficulties in establishing homologies among other gynoecia of Sapindales, we opted to not include these features in this analysis.

Information on different carpel zones is scarce and scattered among Sapindaceae, considering the high diversity of the family (Table 1). For the early diverging lineage, Xanthoceroideae, there are no detailed studies on the development of the inner morphological surface of carpels (except for ovules, Zhou and Liu 2012, and for *Xanthoceras*, Zhou et al. 2019). In Hippocastanoideae, *Handeliidendron* is syncarpous to a large extent, but the available stages (in SEM) are insufficient to define the zones correctly (Cao et al. 2006), similar to *Xanthoceras* (Xanthoceroideae, Zhou et al. 2019) and *Eurycorymbus* (Dodonaeeideae, Cao et al. 2017; Table 2). A symplicate zone is discernable from early stages in *Handeliidendron* and *Eurycorymbus* (Cao et al. 2006, 2017). The *Acer saccharum* Marsh. (Hippocastanoideae) gynoecium is syncarpous. In the apocarpous zone (Table 2), its two long stigmatic branches are asymplicate and unite postgenitally lower down to form the short style through the intertwining of trichomes in its margins. At the centre of this short style a large canal is formed (Peck and Lersten 1991a). In Dodonaeeideae, Weckerle and Rutishauser (2003) showed in detail a mostly syncarpous gynoecium for four species of *Averrhoidium* (Fig. 1a, e, ii, iii; Table 2). At the level of the ovary, an outer median dorsal furrow is present on each carpel, but these do not represent zones of fusion but early developing loculicidal dehiscence lines. Above the symplicate zone, carpels are postgenitally united through the interlocking of marginal papillae (“The three sutures are unicellular papillae”, Weckerle and Rutishauser 2003, p. 781). The style is postgenitally fused for most of its length and the stigma is asymplicate (Fig. 1a, e, i''). Interestingly, in carpelodes of male flowers, the styles are not postgenitally united and free in the upper apocarpous zone. A stigmatic head is likely present in *Averrhoidium dalyi* Acev.-Rodr. & Ferrucci

at the tip of the stigma, where the papillae from contiguous carpels meet in the centre (Tables 2 and 3; Weckerle and Rutishauser 2003).

Among the Sapindoideae, additional studies point to a mostly syncarpous gynoecium. *Delavaya* (Cao and Xia 2009) has only a short apocarpous zone at the tip of carpels. For *Koelreuteria* spp. and Paullinieae more detailed studies are available. All *Koelreuteria* taxa studied so far have (*K. elegans* subsp. *formosana* (Hayata) F.G. Mey: Avalos et al. 2019) or appear to have (*K. paniculata* Laxm., *K. bipinnata* Franch.: Cao et al. 2018; Ronse De Craene et al. 2000) an upper apocarpous zone restricted to part of the stigmatic region that is postgenitally fused. Similar to *Averrhoidium*, the upper part of the stigma in *K. elegans* is asymplicate, and carpels are postgenitally united only laterally by the interlocking of marginal trichomes. In *K. paniculata*, the incomplete fusion of the inner part of each carpel flank makes the epidermis of adjacent carpels partially discernable as so-called “septal cavities”. These corresponds functionally to PTTT, as also observed in *K. elegans* (Avalos et al. 2019; Ronse De Craene et al. 2000). Also, similar to *Averrhoidium*, an outer median dorsal furrow is present in the style and along each of the three carpels making up the ovary, which also correspond to dehiscence lines developing early in each locule. By comparison these are much deeper furrows in *Koelreuteria* considered to be a putative synapomorphy for the genus (Ronse De Craene et al. 2000). The taxa analysed in Paullinieae so far are mostly syncarpous. Only in the stigmatic region a short apocarpous zone develops (Fig. 1a, j). Apparently, it is much shorter than in *Koelreuteria*, but detailed studies on the inner surfaces of the stigma are needed for these groups (Table 2). Carpels appear free in the stigma in most of the taxa analysed in Paullinieae (Fig. 1a, i’; Weckerle and Rutishauser 2005) and apparently postgenitally fused (or contiguous) only in *Paullinia clavigera* Schltld. Also, similar to *Koelreuteria elegans* and *Averrhoidium*, an asymplicate zone is apparently present in the stigmatic region in *Urvillea Ulmacea* Knuth, *P. alata* G. Don, *P. pachycarpa* Benth. and *P. aff. caloptera* Radlk. (Table 3).

In Simaroubaceae there are few detailed studies on the gynoecium. It is interesting to highlight that free carpels (see picture in Online Resource 3) were a main morphological feature used to characterize the former Simarouboideae in Engler’s system (see “Introduction”). Hence current morphological descriptions of the family (e.g., Clayton 2011) consider the gynoecium as having carpels “distinct or connate basally, occasionally connate axially” at the ovary level, one can suspect that a mostly apocarpous gynoecium (i.e., with carpels free or postgenitally fused for most of their length; Fig. 2a, a’, b, b’) is the common structural pattern that predominates in the family. A further aspect that reinforces this assumption is that fruitlets commonly separate early

in development, usually as “samaroid or drupaceous mericarps” (Fig. 3a, b; Clayton 2011). In fact, the few detailed structural studies available corroborate this assumption in most cases. Only male flowers of taxa belonging to the earliest diverging lineages of the family have been studied, yet carpelodes with poorly developed ovary and styles are completely apocarpous and free in *Castela tweedii* Planch. and *Picrasma quassioides* (D. Don) Benn. (tribes Casteleae and Picrasmateae, respectively; Ramp 1988). Morphological studies showed carpels completely apocarpous for *Picrolemma* (unplaced Simaroubaceae), except for a basal union to the gynophore (see picture in Online Resource 3; Devecchi et al. 2018). Other Simaroubaceae also show carpels without intercarpellary fusion at the ovary level (*Brucea*, tribe Leitnerieae; Nair and Joshi 1958; Nair and Sukumaran 1960) or for most of their length (Fig. 2a, b i’, i_b). In the last case, carpels can be congenitally united at the centre from the level of the gynophore up to the base of the ovary (the latter up to the level of the locules, but without a symplicate zone; Fig. 2a, a’, b, b’, c, d, iii, iii’, iii’’) as found in *Simaba glabra* Engl., *S. suffruticosa* Engl., *S. cedron* Planch. and *S. trichilioides* A. St.-Hil. (tribe Simaroubeae: Alves et al. 2017, these species along with several other ones in *Simaba* are currently placed in *Homalolepis*: Devecchi et al. 2018). Carpels fused only to the common gynophore (this being usually considered the “synascidiate zone” by Ramp (1988)) are found in *Ailanthus glandulosus* Desf., *A. excelsus* Roxb., *A. malabaricus* DC. [= *A. triphysus* (Dennst.) Alston], *A. grandis* Prain (tribe Ailanthae), *Quassia amara* L., *Samadara indica* Gaertn., and *S. lucida* Wall. (Fig. 2a, c; Simaroubeae: Endress et al. 1983; Nair and Joseph 1957; Ramp 1988). Above this short congenitally fused zone, carpels are apocarpous in all taxa (Table 2). At the style level, carpels can be either free (Fig. 2b, b’, i_a; e.g., *Brucea sumatrana* Roxb., *Soulamea pancheri* Brongn. & Gris: Clayton 2011; Ramp 1988) or postgenitally fused (Fig. 2a, a’; *Ailanthus* spp., *Q. amara*, *Simaba glabra*, *S. suffruticosa*, *S. cedron*, *S. trichilioides*, *Samadara indica* and *S. lucida*). At the stigmatic level, carpels are usually described as free (Fig. 2a, i’; e.g., *B. sumatrana*, *Ailanthus* spp., *S. pancheri*: Clayton 2011), but there are also taxa with postgenitally fused stigmas, forming a stigmatic head (Fig. 2a, i; *Q. amara*, *Simaba glabra*, *S. suffruticosa*, *S. cedron*, *S. trichilioides*, *Samadara indica*, *S. lucida*: Alves et al. 2017; Nair and Joseph 1957; Nair and Joshi 1958; Narayana and Sayeeduddin 1958; Ramp 1988; Table 2). *Soulamea pancheri* is the sole taxon of Simaroubaceae (in its current circumscription) that was described as syncarpous up to the apex of the ovary locules, with a symplicate zone at its distal part (Ramp 1988). However, this finding should be taken with caution, as Ramp (1988) only analysed a young fruiting carpel of this species and not its ontogeny. In contrast, Devecchi et al. (2018) considered the carpels of the same taxon as apocarpous based on

a morphological analysis. Further detailed studies on flowers of Simaroubaceae should clarify these unclear aspects of gynoeceum structure of the family (G.G.N. Alves in prep.). Male flowers of *Simarouba amara*, *Soulamea pancheri*, *A. excelsus* have a similar pattern of carpel development as *Castela* and *Picrasma*, in the sense that carpelodes are apocarpous. Additionally, when compared to female flowers of the first three taxa, carpelodes specifically lack the postgenital fusions at corresponding levels of fertile carpels (Nair and Joseph 1957; Nair and Joshi 1958; Ramp 1988).

The gynoeceum of Rutaceae has been studied in detail for a broad sample of taxa (Table 1). Among the Cneoroideae, the gynoeceum has been found to be syncarpous for *Harrisonia brownii* A.H.L. Juss and *Cneorum tricoccon* L. but the extent of each carpellary zone was not established for the latter species: the apex of the ovary and style seems to be formed by postgenital fusion, but without a stigmatic head (free stigmatic lobes; Caris et al. 2006; Table 2). Also, in *C. tricoccon*, similar to *Koelreuteria paniculata* (Sapindaceae; Ronse De Craene et al. 2000), “septal cavities” have been found, but not in the style. They occur on the lateral flanks of the ovary and are similarly the product of the incomplete fusion between the three adjacent carpels, thus representing their morphological surfaces. In contrast to *K. paniculata*, these “cavities” are not secretory (Caris et al. 2006). Current morphological descriptions of the eight genera of Cneoroideae point out to a mostly syncarpous gynoeceum, except for *Dyctioloma* (Kubitzki et al. 2011).

In subfamily Rutoideae, there is a wide variation in the extent of fusions among carpels. An exception to this variation among Rutoideae occurs in the tribe Aurantieae (the “*Citrus*” group, formerly subfamily Aurantioideae of Engler 1931) where carpels have a stable architecture in the sense that they are mostly syncarpous, usually up to the apex of the style (Fig. 1a, f; Table 2). A short apocarpous zone is restricted to the stigmatic region, which is usually postgenitally fused (Table 2; Gut 1966; Johri and Ahuja 1957; Leins 1967; Ramp 1988; Tilak and Nene 1978; Tillson and Bamford 1938). This stability has been associated with conservative fruit traits of Aurantieae, as for instance fruitlets that never separate at maturity (fruit indehiscent, baccate; Tilak and Nene 1978; Tillson and Bamford 1938; Wei et al. 2015).

In contrast, all other Rutoideae groups show a wider variation in gynoeceum architecture, previously described in ontogenetic analyses (Table 2; El Ottra et al. 2013, 2019; Endress et al. 1983; Gut 1966; Ramp 1988; Wei et al. 2011, 2015). In the mostly apocarpous groups, carpels are congenitally united only at the base of the ovary, including the gynophore level when formed (Table 2; Fig. 2a, a', c–f, iii, iii'; El Ottra et al. 2013, 2019; Gut 1966; Ramp 1988; Souza et al. 2003; Wei et al. 2011, 2015). More rarely, in *Boenninghausenia* (Fig. 2a, c, iii'), *Zanthoxylum simulans* Hance, and likely most other species of the genus, carpels

are congenitally fused only at the gynophore level (Fig. 2b, g, iii; Beurton 1994; Ramp 1988). Similar to the apocarpous Simaroubaceae, a symplicate zone never develops. Above the base of the ovary, carpels are entirely apocarpous (free), with plicate margins (Fig. 2a, a', i"). In the apocarpous zone (Table 2), carpels are postgenitally fused in nearly all taxa (Fig. 2a, a', i), rarely free (*Z. simulans*; Fig. 2b, b'). At the stigmatic level, carpels are mostly postgenitally fused, forming a stigmatic head (Fig. 2a, a', i), more rarely free (in *Z. simulans*—Fig. 2b, b', i_a; *Ravenia spectabilis* (Lindl.) Planch. ex Griseb., *Agasthoma* and *Dictamnus*—Fig. 2a, i'; Beurton 1994; El Ottra et al. 2013, 2019; Gut 1966; Ramp 1988; Souza et al. 2003; Wei et al. 2011, 2015). In other Rutoideae not placed in Aurantieae, syncarpy may occur, though in a lesser degree (Table 2; Fig. 1a, e; Gut 1966; Ramp 1988). The diversity in gynoeceum fusions found in most taxa of Rutoideae indicates that in most cases carpel fusion is a labile feature in the evolution of this group, unless it is associated later in development with specific indehiscent fruit types, such as those of Aurantieae. In fact, carpel fusion has been found to be interspecifically polymorphic in one species, *Rauia resinosa* Nees & Mart. (Galipeae; El Ottra et al. 2019). Also, fruit structure can be quite variable even when comparing narrow taxonomical groups of Rutoideae, as for instance the sister genera of Galipeae, *Adiscanthus* and *Hortia*, with dry fruitlets separating from early stages (Fig. 3d) and a baccate indehiscent fruit, respectively (El Ottra et al. 2019, pers. obs.; Groppo et al. 2008).

In the family Meliaceae there are few detailed studies on the gynoeceum, and none involving the development of the inner morphological surfaces of carpels (Bachelier and Endress 2008). For Cedreloideae (*Cedrela*, *Toona* and *Swietenia*) there are studies that show some developmental stages of carpels surfaces in SEM (Gouvêa et al. 2008a, b). These studies show evidence of syncarpy, but the extent of development of different zones could not be observed. Except for carpel apices, which appear to be postgenitally fused forming a stigmatic head (Bachelier and Endress 2009), other structural studies also showed evidence for a syncarpous gynoeceum for both Melioideae and Cedreloideae taxa (Lal 1994; Murty and Gupta 1978a, b; Nair 1958, 1959a, b, 1962, 1963; Nair and Kanta 1961; Narayana 1958, 1959; Souza et al. 2001, 2002), with a symplicate zone likely present in the upper part of the ovary (Table 2).

Our ontogenetic study of *Trichilia pallens* confirms previous assumptions (for Meliaceae, Bachelier and Endress 2008) that its gynoeceum is syncarpous, with extensive symplicate and synascidiate zones (Figs. 4 and 5). A very short apocarpous (free) and asympicate zone is formed only at the very tip of the stigma (Figs. 1a, d, i", 4a, b and 5d), as seen from young stages (Fig. 5a). Lower down, carpels are symplicate from the stigma up to the upper third of the ovary. The synascidiate zone comprises the lower two thirds

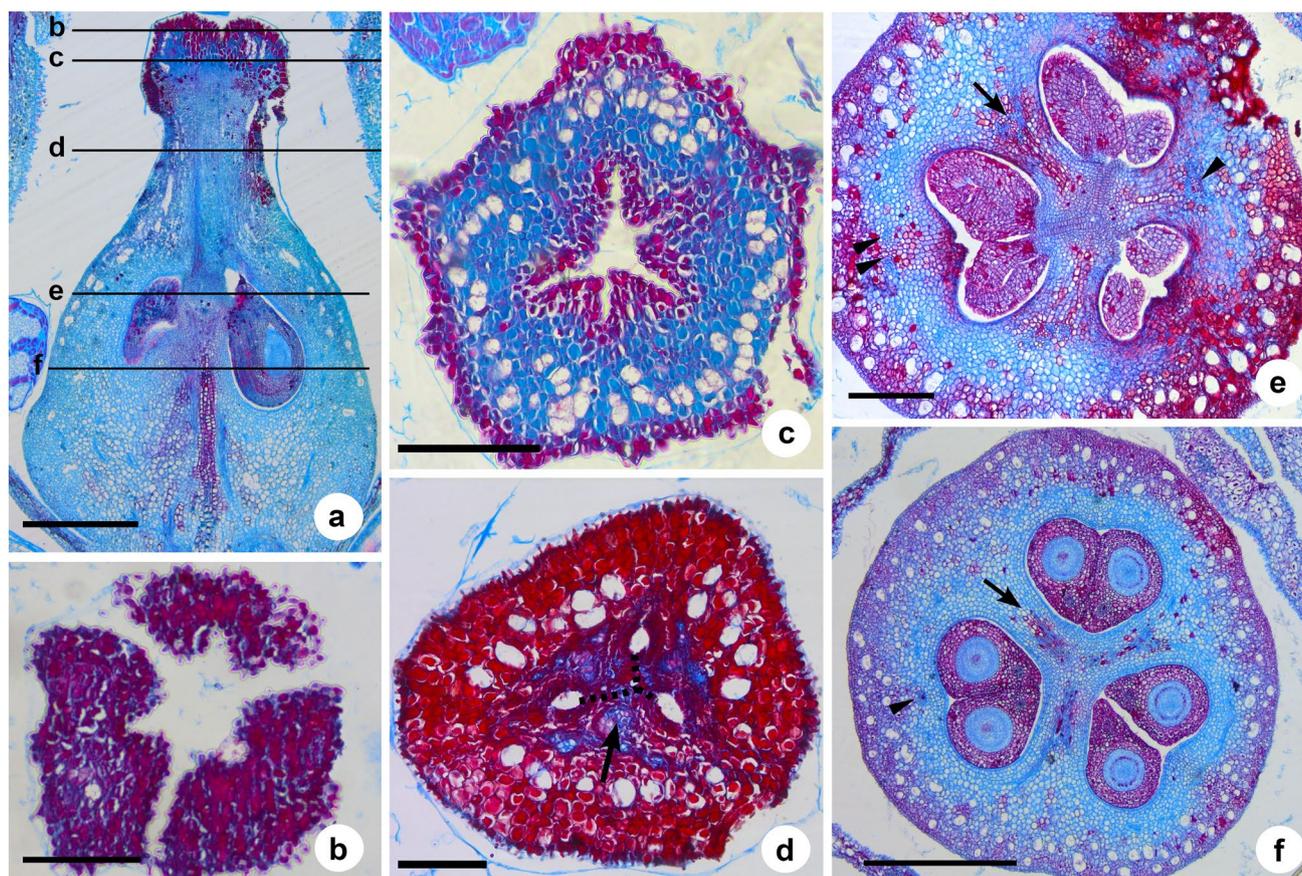


Fig. 4 Photomicrographs of microtome sections of the anthetic gynoecium of *Trichilia pallens* (Meliaceae). Hatched lines indicate postgenitally fused regions. **a** Longitudinal section. **b–f** Transverse sections. **b** Tip of the stigma. **c** Mid-level of the stigma. **d** Style, with

three styler canals. **e** Distal level of the ovary. **f** Lower half of the ovary. Arrows: synlateral bundles; arrowheads: median main dorsal bundles. Scale bars: **a, f** 500 μm ; **b, c, e** 200 μm ; **d** 100 μm

of the ovary (Figs. 4a, c–f and 5b–e; Table 2). At the lower half of the stigmatic region a central star-shaped furrow is formed (lining the inner limits of the unfused morphological surfaces of carpels), which closes partially lower down in the style, forming three canals, one per carpel. Carpels are postgenitally fused along part of their ventral slit and centrally in the style (Figs. 4c, d and 5b, d). In this same region, distally of the ovary level, carpels are tightly contiguous by the interlocking of their papillate epidermis (in the sympligate zone; Fig. 4e).

As general morphological descriptions of the family considered the gynoecium as syncarpous in Meliaceae (Harms 1940; Pennington and Styles 1975), one can suspect that a mostly syncarpous gynoecium, with intercarpellary congenital fusion for most of the carpel length, is the common structural pattern that predominates in the family. A further aspect that reinforces this assumption is that fruiting carpels either separate late in development (capsules, widespread in Melioideae), or fruits are indehiscent (berries and drupes; Gama et al. 2021a), unlike those of the closely

related families of Sapindales, Rutaceae and Simaroubaceae. In the latter two families fruits separating as fruitlets from early stages are a widespread feature (Fig. 3a–d; except for Aurantieae in Rutaceae). This is likely facilitated by the high degree of apocarpous in the anthetic gynoecium of most taxa of these two families (El Ottra et al. 2013; Endress et al. 1983). These fruits are usually described as schizocarpic, separating in various types of mericarps (e.g., drupeaceous, lenticular) or as winged fruitlets (Alves et al. 2022; Devecchi et al. 2018; Paschoalini et al. 2022; Kubitzki et al. 2011). But since schizocarps and mericarps are usually associated with a syncarpous gynoecium (e.g., Leins and Erbar 2010), these terms should be revised. Such apocarpous fruits may be better termed as “fruitlet-aggregates”, with a variety of types of fruitlets (e.g. follicles and drupelets), as commonly found in Simaroubaceae and apocarpous Rutoideae, respectively (Fig. 3; Kubitzki et al. 2011; Leins and Erbar 2010). With the available evidence, carpel structure indicates a closer relationship of Simaroubaceae to Rutaceae, and not to Meliaceae, due to the mostly apocarpous gynoecium

predominantly found in the first two families. The molecular study of Lin et al. (2018) supports this view (but see also Gama et al. (2021a) and Mueller-Riehl et al. (2016) for a contrasting view). Still, further ontogenetic studies with more taxa, especially in Simaroubaceae and Meliaceae, are needed in order to corroborate these ideas.

The functional advantage of mostly apocarpous carpels is usually associated to the development of a compitum at the postgenitally fused carpel tips, as discussed in the next section. Another possible functional advantage in such gynoeceum architecture is that fruitlets separating from early stages of development (as found in Rutaceae and Simaroubaceae) may decrease the impact of herbivory on the entire fruit. Damaging an individual fruiting carpel may be less harmful to the seed set and plant fitness in general, than damaging an entire syncarpous fruit (Endress et al. 1983), depending on the ecological conditions where the plants grow and evolve. In fact, recent studies have found that herbivory in reproductive plant traits may be a more important selective force to the outcome of structural evolution than previously considered (Jogesh et al. 2017; McCall and Irwin 2006).

Pollen tube transmitting tract and compitum

The pollen tube transmitting tract (PTTT) is formed on the primary inner surface of carpels, or at least on most part of it. In a syncarpous gynoeceum a compitum is usually found internally in the symplicate zone of carpels (Endress 1994). Among the Sapindales, three main types of PTTT may occur: the “open”, half-closed” and the “closed” PTTT (following the classification of Hanf (1936); also in Endress (1994)). These types can be best recognized in histological sections of material correctly fixed for that purpose (fixatives that do not use alcohol in its chemical constitution), and they are presented in Table 3, accordingly to their occurrence in each family. Regardless of these three main types, other variations may occur. These include alterations in the position of the PTTT (e.g., Fig. 1a, i, i'). Also, variations in relation to the level of formation of the internal compitum and its communication to the outer surfaces through stigmatic papillae are found, where it has been considered as an “external compitum” in some taxa of Sapindales. In fact, “minimal structural differentiation between stigma and transmitting tissues” has been found in taxa of the order (Bachelier and Endress 2008, 2009; Bachelier et al. 2011). However, this information is not available for all families (Table 3).

For the Nitrariaceae this is well reported (Tables 1 and 3). At the level of the stigma, three lateral papillate areas (secretory papillae, receptive areas) alternating with three non-papillate and non-secretory areas are found in all three genera of the family. At this level, the lateral papillate areas of the stigma are in continuity with the inner morphological

surfaces of carpels where the PTTT is formed, on the lateral and ventral sides of the three postgenitally fused carpels (Fig. 1a, i'). Due to this continuity between the outer papillate areas and inner PTTT, Bachelier et al. (2011) considered that at this level the compitum is partially external and internal.

In Kirkiaceae both PTTT and compitum are also well described (Bachelier and Endress 2008). An external compitum is formed only at the level of the postgenitally fused stigmas (stigmatic head), which lower down separates in four strands of PTTT (one per carpel) positioned in the inner angle of the ventral slit in the plicate zone of carpels (Fig. 1b, i, ii'). In the sister group of Kirkiaceae, the clade formed by Anacardiaceae and Burseraceae, the PTTT is found in a similar position, for most of its length (Fig. 1b, i, c, ii; Bachelier and Endress 2007, 2009; Gonzalez 2016; Tölke and Demarco 2020; Tölke et al. 2021). However, distally, the formation of an external and/or internal compitum varies among families. Since the Burseraceae present postgenital fusion of the style and stigma, a stigmatic head with an external compitum can be formed (Fig. 1b, i; Bachelier and Endress 2008, 2009). In contrast, many Anacardiaceae do not present a compitum, either because carpels are not usually fused at the tips, or, because of the PTTT disposition that does not allow continuity between them (Bachelier and Endress 2009; Gonzalez 2013, 2016; Tölke and Demarco 2020; Tölke et al. 2021). More rarely an external compitum (complete or incomplete) appears to be formed in the stigmatic region when stigmas are contiguous (*Spondias dulcis*, *S. macrocarpa*) or fused in the distal part of the styles and/or stigmas (*Dracontomelon*, *Semecarpus*, *Amphipterygium*, *Pistacia*). Though a symplicate zone is found in Burseraceae and some Anacardiaceae (*Pistacia*, *Schinus* and *Semecarpus*) an intragynoeceal compitum “does not appear to be present” (Bachelier and Endress 2009). Interestingly, the PTTT in some pseudomonomerous species of Anacardiaceae is present at the tip of carpels but vanishes downwards to the style base (or apex of the ovary) in sterile carpels (Bachelier and Endress 2007, 2009; Gonzalez 2013, 2016; Tölke and Demarco 2020; Tölke et al. 2021; Wannan and Quinn 1991).

In Sapindaceae, limited information is available for the family in general, but PTTT features are well described for some members. In *Acer saccharum* (Hippocastanoideae) the free and long stigmatic lobes are papillate on their adaxial side, and these (unicellular) papillae are in continuity with the papillate canal (PTTT) formed lower down in the style. This single canal has a large lumen (as seen in transections) and is lined by the single-layered secretory papillate epidermis. It runs downwards to the style and ovary, up to the level of the obturator (Peck and Lersten 1991a). Peck and Lersten (1991a) considered that the compitum is internal, formed only at the ovary level (likely the symplicate zone), based on some pollen tube growth analyses. However, we do

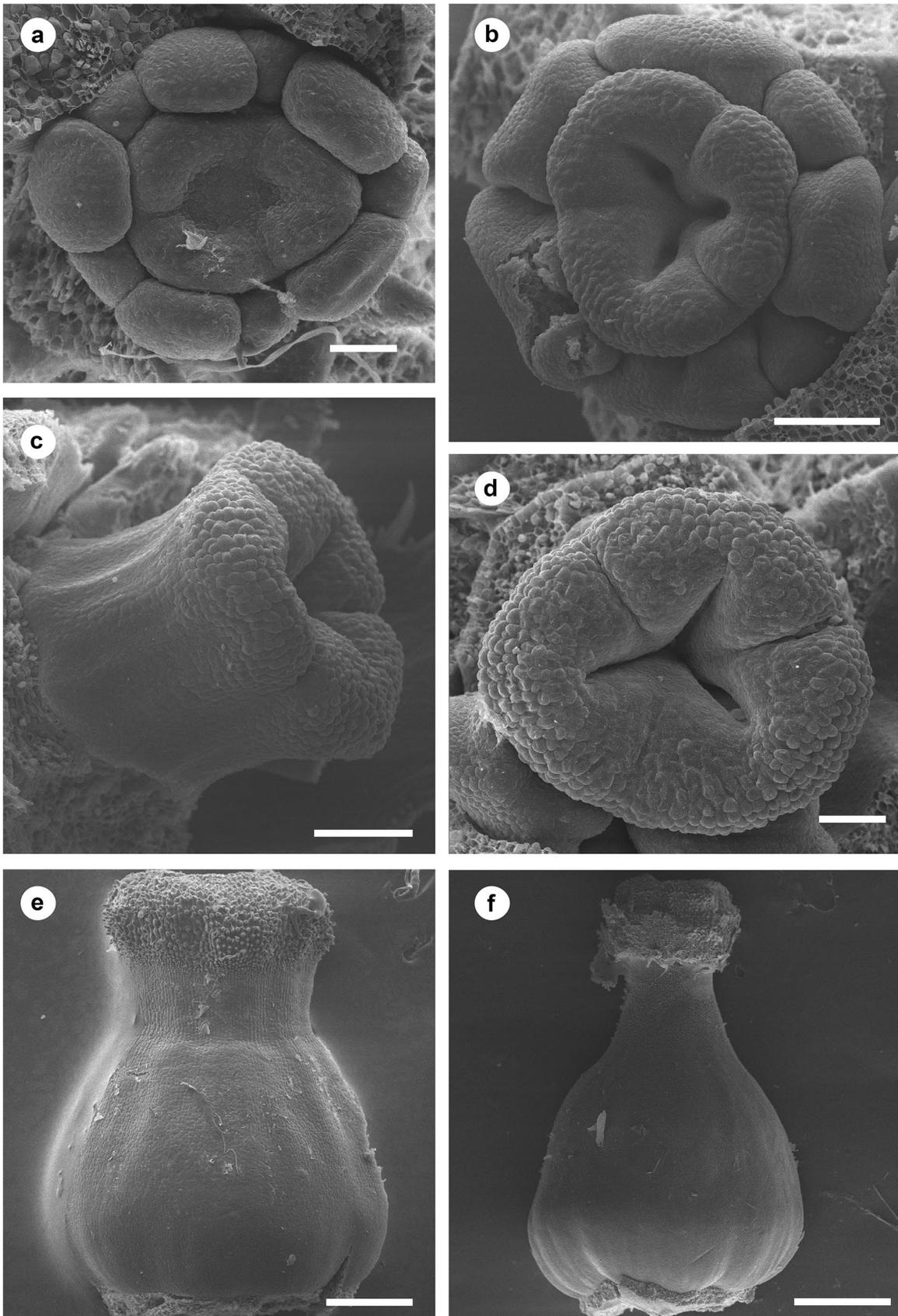


Fig. 5 Carpel development of *Trichilia pallens*, Meliaceae (SEM micrographs). **a** Three young separate primordia. **b** Young carpel with a common base, and beginning of differentiation of stigmatic papillae. **c** Young style starts to elongate. **d** Top view of the young stigma and symplicate zone. **e** Young gynoecium, with ovary expanding and elongating stigmatic papillae (compare with **c**). **f** Anthetic gynoecium. Scale bars: **a, d** 50 μm ; **b, c** 100 μm ; **e** 200 μm ; **f** 500 μm

not see why a compitum at the style level could not also be considered. The large stylar canal of the PTTT, together with “incomplete carpel closure” (*i.e.*, postgenitally united styles) was considered a trait related to wind pollination in *Acer*.

Averrhoidium (Dodoneoideae) and *Koelreuteria* (Paullinieae) share similarities regarding the PTTT organization in the distal part of the stigma, comparable to Nitrariaceae (see above). Although not equally described in all studies, the PTTT in these Sapindaceae taxa represents a system of three external lateral papillate areas of the stigma continuous with the inner PTTT on the lateral and ventral sides of the three postgenitally united asymplectate carpels (Avalos et al. 2019; Ronse De Craene et al. 2000; Weckerle and Rutishauser 2003). So, this continuity between the outer papillate areas and inner PTTT can be considered a compitum that is partially external and internal at this level, as similarly found in Nitrariaceae. From the base of the stigma and style (symplicate zone) an internal compitum also develops in *Averrhoidium* and *K. elegans*, since the three stylar canals (PTTT) alternate with the locular cavities. All these canals and cavities are contiguous at the centre, forming a central and relatively wide canal full of secretion in the style (Avalos et al. 2019; Weckerle and Rutishauser 2003; Table 3). However, in *K. paniculata* the PTTT form three narrow canals that alternate with three locular furrows but do not form a wide canal. Apparently in this species the PTTT becomes “closed” in the style, but is still in contiguity at the centre, forming likely a compitum (Ronse De Craene et al. 2000). For tribe Paullinieae (in *Cardiospermum*, *Paullinia* and *Serjania*), the papillose adaxial stigmatic surface is also in continuity with the PTTT lower down, usually represented as a large and single stylar canal lined with a secretory epidermis and a lumen filled with secretion. However, here we find the “open”, “half-closed”, and “closed” PTTT, since the PTTT can be respectively developed as (1) a canal lined by secretory papillae or hairs only (*Paullinia alata*, *P. obovata*), (2) these same features plus two subepidermal layers of elongated secretory cells (*P. pachycarpa*, *P. dasystachya*, *C. halicacabum*, *S. altissima*), or even (3) a solid tissue with mucilaginous cells (*P. clavigera*, *P. aff. caloptera*). The compitum is formed at the level of the style due to this single central canal or mucilaginous tissue that is formed in the symplicate zone of the carpels (Weckerle and Rutishauser 2005). In fact, a “hollow style” is considered by Stevens (2001 onwards) as a putative synapomorphy for

the clade formed by Hippocastanoideae, Dodoneoideae and Sapindoideae.

In Simaroubaceae data are scarce, but the PTTT position is similar to the one found in Kirkiaceae, Burseraceae and Anacardiaceae. In *Ailanthus glandulosa* (Ailanthaceae), *Quassia amara*, *Simaba glabra* *S. suffruticosa*, *S. cedron*, and *S. trichilioides* (Simaroubeae, the four latter currently species of *Homalolepis*) each carpel has one strand of PTTT in the style, positioned for most of its length in the inner angle of the postgenitally fused ventral slit. However, contrary to most Burseraceae, the PTTT is present solely in the plicate zone of carpels (Fig. 2a, i', b, i_a). An internal compitum has the potential to be formed in the distal part of the postgenitally fused style as a central tissue just below the stigmatic lobes or stigmatic head (Fig. 2a, i; Alves et al. 2017; Ramp 1988). In the species with stigmatic head (Simaroubeae: Alves et al. 2017; Nair and Joseph 1957; Ramp 1988) it is assumed that an external compitum is absent, although it might occur. Further studies on pollen germination on the stigma are necessary to corroborate this idea. In *Q. amara*, PTTT and compitum were discernible only in anthetic flowers (Ramp 1988).

In Rutaceae, the PTTT position and level of formation of the compitum in mostly apocarpous Rutoideae is very similar to most Simaroubaceae. In fact, this kind of gynoecium architecture is associated with the distal formation of a compitum in the postgenitally fused style/stigma (Fig. 2a, i), having the advantage of enhancing pollen tube selection in apocarpous gynoecia, as already extensively discussed (Bachelier and Endress 2008, 2009; Endress et al. 1983; Matthews and Endress 2005; Matthews et al. 2012; Ramp 1988). As a symplicate zone is absent in these groups, the PTTT is always positioned in the plicate zone at the inner angle of the postgenitally fused ventral slit for most of its length (Fig. 2i", b, i_a; Ramp 1988). As most species of apocarpous Rutoideae have a stigmatic head (Fig. 1a, i; Beurton 1994; El Ottra et al. 2013, 2019; Endress et al. 1983; Gut 1966; Pirani et al. 2010; Ramp 1988; Souza et al. 2003; Wei et al. 2011, 2015) an external compitum could exist but should be clarified by further functional studies. Still, though some taxa have a central canal at some levels of the style, this is neither secretory nor filled with secretion (not PTTT; El Ottra et al. 2013, 2019; Ramp 1988). It represents regions of incomplete postgenital fusion of carpels at the centre, as shown for *Pilocarpus*, *Dictamnus*, *Boronia*, some Galipeinae, *Skimmia* and *Phellodendron* (the latter two syncarpous taxa: El Ottra et al. 2019; Ramp 1988). *Dictamnus* is the sole exception among the apocarpous Rutoideae with a “opened” PTTT at the distal part of the style, represented by one narrow canal at the inner angle of the partially unfused ventral slit. Lower down in the style it follows the same pattern of the apocarpous groups.

In the syncarpous groups of Rutoideae PTTT and compitum were found to be highly similar among the Aurantieae (in 29 genera: Gut 1966; Ramp 1988; Tilak and Nene 1978; Tillson and Bamford 1938; Table 3). In all members of this tribe the PTTT is mostly structured as styler canals, one per carpel, with its epidermis lined with secretory trichomes. These canals become contiguous with the hairy obturator. The styler canals are present mostly in the symplicate zone of the style and ovary. They can eventually become centrally continuous also forming a central canal, and the PTTT then becomes star-shaped at the tip of the style [*Citrus trifoliata* L., *Murraya paniculata* (L.) Jack] or more rarely only a single canal is formed throughout its length [*Fortunella japonica* (Thunb.) Swingle = *Citrus japonica* Thunb. as currently accepted]. In this last case a compitum is formed throughout the style. Except for *F. japonica*, most other Aurantieae are considered to have a compitum only at the distal level of the style (Ramp 1988). In contrast, other syncarpous Rutoideae not placed in Aurantieae have a PTTT in a similar position and type to the apocarpous Rutoideae, but run downwards to the symplicate zone of the ovary. For most taxa of these groups a compitum was found only distally in the style. The syncarpous Cneoroideae taxa described so far (*Harrisonia*, Ramp 1988) have one narrow canal per carpel positioned at the inner angle of the partially unfused ventral slit, that runs from the upper plicate zone downwards to the symplicate zone of the ovary. A compitum was found only at the stigmatic level. It is not clear why authors did not describe the formation of the compitum at the symplicate zone for the syncarpous taxa of Rutaceae, since it is usually found in this region of the syncarpous gynoecium in general (Endress 1994). Further functional studies should clarify this question.

For the Meliaceae, scarce reports are available. Styler canals are widespread in the family but only the studies of Narayana (1958, 1959) and Souza et al. (2001, 2002) found evidence of secretory activity in the epidermis of the styler canals (*i.e.*, PTTT). In all other taxa where styler canals were described, secretory tissue was not found or was not mentioned (this study, Fig. 4d; Lal 1994; Murty and Gupta 1978a, b; Nair 1962, 1963; Narayana 1958, 1959). This absence of secretory tissue could be explained by three hypothesis: (1) flowers in bud stage (as sectioned for these studies) are too young to present the secretory layer(s) of PTTT, which will develop in the anthetic gynoecium (as previously reported for other Sapindales by Ramp (1988)); (2) the flowers analysed could be structurally bisexual, but in fact functionally unisexual, and thus the lack of secretory tissue in styler canals could indicate that the gynoecium is not fertile (well-developed carpelodes are widespread in Meliaceae, Styles 1972); (3) styler canals in these taxa represent regions of incomplete postgenital fusion of carpels, and not PTTT, as found for some taxa of Rutoideae (see

above). We think the third hypothesis is the less likely, due to the apparent high degree of syncarpy found in Meliaceae carpels so far.

Among subfamily Cedreloideae, styler secretory canals are apparently present (Table 3). In the distal part of the style/stigma it forms a single central, star-shaped canal, with the number of “arms” of the star equal to the number of carpels. However, for most of the style length, PTTT separates as one styler canal per carpel (*Swietenia*, *Cedrela*, *Toona*, *Chukrasia*). In *Swietenia mahogany* a secretory papillate epidermis lines the styler canals (Lal 1994; Murty and Gupta 1978a; Narayana 1958). Among the Melioideae the same pattern as described for Cedreloideae canals was herein found in *Trichilia pallens* (Fig. 4c, d), *Melia azedarach*, and likely also for *M. birmanica* and *M. composita* (Murty and Gupta 1978b; Narayana 1958). Additionally, our finding in *T. pallens* show the three styler canals running downwards to the symplicate zone of the ovary, where they become contiguous with the locules (Fig. 4d, e). No secretion or secretory tissue was found within the styler canals of this species. Other Melioideae apparently present slightly different patterns and are described as having one single styler canal (Murty and Gupta 1978b; Narayana 1958, 1959; Souza et al. 2001, 2002). *Walsura* and *Hynaea* have very similar PTTT with two styler canals lined with long papillae (Narayana 1958, 1959). An internal compitum was assumed to be formed in the symplicate zone of carpels of *Trichilia catigua*, *T. elegans*, and *T. pallida* by Souza et al. (2001), but we do not see why it could not be considered to occur also throughout the single style canal (PTTT) in these and other species with similar canals. Further functional studies integrating the ontogeny of the styler canals concatenated with pollen germination studies should clarify all these questions regarding PTTT and compitum structure in Sapindales.

Participation of the floral apex in the gynoecium architecture

The floral apex is either used up completely with the development of the carpels, or can be integrated as part of the gynoecium architecture in some groups of angiosperms (Endress 2019), such as Sapindales. This could represent an “apomorphic tendency” for the order (following the definition of Endress and Matthews (2012)) since it is present in several taxa from six of its families (Table 3). In the early diverging family Biebersteiniaceae, it is present in the basal part of the fused carpels, but also centrally protruding in the apocarpous region of the ovary (in *Biebersteinia orphanidis* Boiss.). The short remnant of the floral apex is apparently enclosed in the ovary, at least in early stages of gynoecium development (see Fig. 2b, c in Yamamoto et al. 2014, and also the scheme in Online Resource 4). In Kirkiaceae, the

floral apex is present in the same position, but is much longer, reaching beyond the distal part of the syncarpous ovary and is covered by the postgenitally fused carpel tips in the anthetic gynoecium (Fig. 1b, b'; Table 3). Additionally, it is considered an integral part of the synascidiate zone of the ovary, as observed for its sister families, Anacardiaceae and Burseraceae (Bachelier and Endress 2008, 2009; Tölke et al. 2021). In the latter two families, the floral apex is also extended in most taxa with multicarpellate gynoecium (Fig. 1c, c'), even in some pseudomonomerous taxa of Anacardiaceae (Bachelier and Endress 2009; Tölke et al. 2021). Its length is more variable in Burseraceae: from the lower half of the ovary up to its distal level (Table 3, for core Burseraceae; Bachelier and Endress 2009). Similar to Kirkiaceae, the floral apex can be “uplifted at the base of free carpel tips”, beyond the synascidiate zone (above the ovary locules; Fig. 1b', l, c', m; *Spondias*, *Pleiogynum*, *Dracontomelon*) or above the ascidiate zone (*Tapirira*), in multicarpellate and pseudomonomerous taxa of Anacardiaceae, respectively (Bachelier and Endress 2009; Tölke et al. 2021). It is not covered by the styles/stigma in most Anacardiaceae with free carpel apices, and thus the floral apex is “exposed at anthesis” (Fig. 1c'), as in *Spondias*, *Pleiogynum*, and *Poupartioopsis* (Spondioideae). Alternatively the floral apex is covered by the united (contiguous or more rarely fused) carpel tips, as in *Spondias dulcis*, *S. tuberosa*, *Dracontomelon*, *T. guianensis* (Fig. 1b'; Spondioideae) and *Beiselia* (early diverging Burseraceae; Bachelier and Endress 2009; Wannan and Quinn 1991; Table 3). In the pseudomonomerous gynoecium of Anacardiaceae the presence and position of the floral apex is a matter of debate, as discussed by Bachelier and Endress (2009). In fact, “a massive remnant of the floral apex” in the gynoecium of Kirkiaceae, Anacardiaceae and Burseraceae (*Beiselia*) is considered a putative synapomorphy or an apomorphic tendency for this clade (Bachelier and Endress 2008, 2009).

In Rutaceae and Simaroubaceae the floral apex is similar to *Biebersteinia orphanidis* (see Online Resource 4, c) and core Burseraceae (Table 3). The floral apex is present at the base of the ovary in most taxa and is always covered by the upper postgenitally fused carpels (Fig. 2a, a', except for *Brucea*, Simaroubaceae, see below). It was similarly considered part of the synascidiate zone of carpels in most studies (Alves et al. 2017; see in El Ottra et al. (2019) Figs. 5a, g, 11a, b; see also Gut (1966) and Guédès (1973) for an extensive discussion; Ramp 1988). It is found in several taxa of Rutoideae (Gut 1966; Ramp 1988), and in most Galipeinae of Rutaceae (El Ottra et al. 2019). In Simaroubaceae it is found in Ailanthaceae, Picramnaceae, Leitneriaceae, and Simaroubeae, (Alves et al. 2017; Nair and Joshi 1958; Ramp 1988). The floral apex of these two families is usually short and slightly different in shape (Table 3; Online Resource 4; Alves et al. 2017; Nair and Joshi 1958; Ramp 1988). More

rarely in Simaroubaceae, in *Brucea sumatrana*, it is long, raised up to the distal level of the ovary (apocarpous zone of carpels, Nair and Joshi 1958; Fig. 2b', i_b). This was also observed in Kirkiaceae and some Anacardiaceae Spondioideae, as mentioned above, but as part of the syncarpous zone of the ovary (Fig. 1b', iii).

Thus, it is interesting to note that the integration of the floral apex in the gynoecium architecture is more widespread in Sapindales than previously thought. It varies both in length, distal shape, and degree of exposure (Table 3). Additionally, its occurrence may be correlated to other features, such as the absence of a symplicate zone, both in apocarpous (Rutoideae, Simaroubaceae, maybe Biebersteiniaceae) and syncarpous groups (Kirkiaceae and Anacardiaceae), with the exception of Burseraceae. (Alves et al. 2017; Bachelier and Endress 2008, 2009; El Ottra et al. 2013, 2019; Gut 1966; Nair and Joshi 1958; Ramp 1988). Finally, its presence may apparently have consequences later in development, since a “central column” (Capuron 1961) or columellas are usually described in fruiting carpels of Biebersteiniaceae (Knuth 1912; Stevens 2001 onwards) and Kirkiaceae (histologically derived from the central region of the synascidiate ovary), from where fruitlets usually detach at maturity (Bachelier and Endress 2008). Although columellas are also described for fruits of many Cedreloideae (Meliaceae; Pennington and Styles 1975) there is not sufficient anatomical work to trace a parallel with the role of the floral apex in the formation of the columellas in these taxa. Further studies aim to better comprehend the consequences of the integration of the floral apex in the gynoecium architecture.

Considering the findings presented so far, we believe that the terminology used to define syncarpous and multicarpellate apocarpous gynoecia in Sapindales should be revised. The general terminology applied for the syncarpous gynoecium (Leinfellner 1950) does not fit well with the many variations found in the construction of the gynoecium in the order (summarized in Figs. 1 and 2), as already observed by Bachelier and Endress (2009). Since part of the syncarpous taxa lack a symplicate zone in the gynoecium, and instead the floral apex continues at its centre (Fig. 1b', c') comparable to mostly apocarpous taxa (Fig. 2a', b', Online Resource 4), we propose a new and more simplified terminology for Sapindales. In our concept a gynoecium should be considered syncarpous when intercarpellary congenital fusion occurs from the carpel bases up to mid-level of the ovary, independent of the inclusion of the floral apex (since the floral apex is congenitally fused to carpels; Endress 2019; Fig. 1). A gynoecium should be considered mostly apocarpous when intercarpellary congenital fusion comprises less than half the length of the ovary. In mostly apocarpous gynoecia described so far in Sapindales, a symplicate zone is not present (Fig. 2). In fact, previous studies considered the gynoecium of many Rutoideae (except Aurantieae) as

“mostly apocarpous” based on the short length of the proximal congenitally fused zone (El Ottra et al. 2013, 2019; Endress et al. 1983). Postgenital union is not included in our concept as it is so variable and labile in Sapindales, and therefore it would be best just to describe the occurring variations than creating a series of new terms. In this sense our concept is similar to Leinfellner (1950), who did not include postgenital union in its terminology for the syncarpous gynoecium.

Still, one could argue that setting such limits between syncarpous and apocarpous gynoecia is arbitrary for Sapindales. In fact, when analyzing the ontogeny of the Sapindales gynoecium it becomes clear that there is a structural continuum between apocarpous and syncarpous in the order, created by the differential growth of the different zones after carpels initiation. That is, a more extensive growth of the apocarpous zone in relation to the syncarpous zone throughout carpel development will give rise to a mostly apocarpous gynoecium (Fig. 2a, b), while a more extensive growth of the syncarpous zone in relation to the apocarpous zone will give rise to a more pronounced syncarpous gynoecium (Fig. 1a–c). Still, we believe that setting such limits are important for two reasons: (1) for the study of character evolution, to understand how and in which direction apocarpous and syncarpous evolved in the order and (2) carpels that are mostly apocarpous have particularities regarding the reproductive biology of the plant, as mentioned in topic 1. They form fruits through very particular ontogenetic pathways, as carpels separate very early in fruit development (the free or postgenitally ovary apices break apart and separate very early, Fig. 3; El Ottra et al., 2013; Gut 1966; Pirani et al. 2010; Ramp 1988; this study). Therefore, plant reproduction follows a particular strategy in groups with mostly apocarpous gynoecium.

Style position in relation to the ovary apex

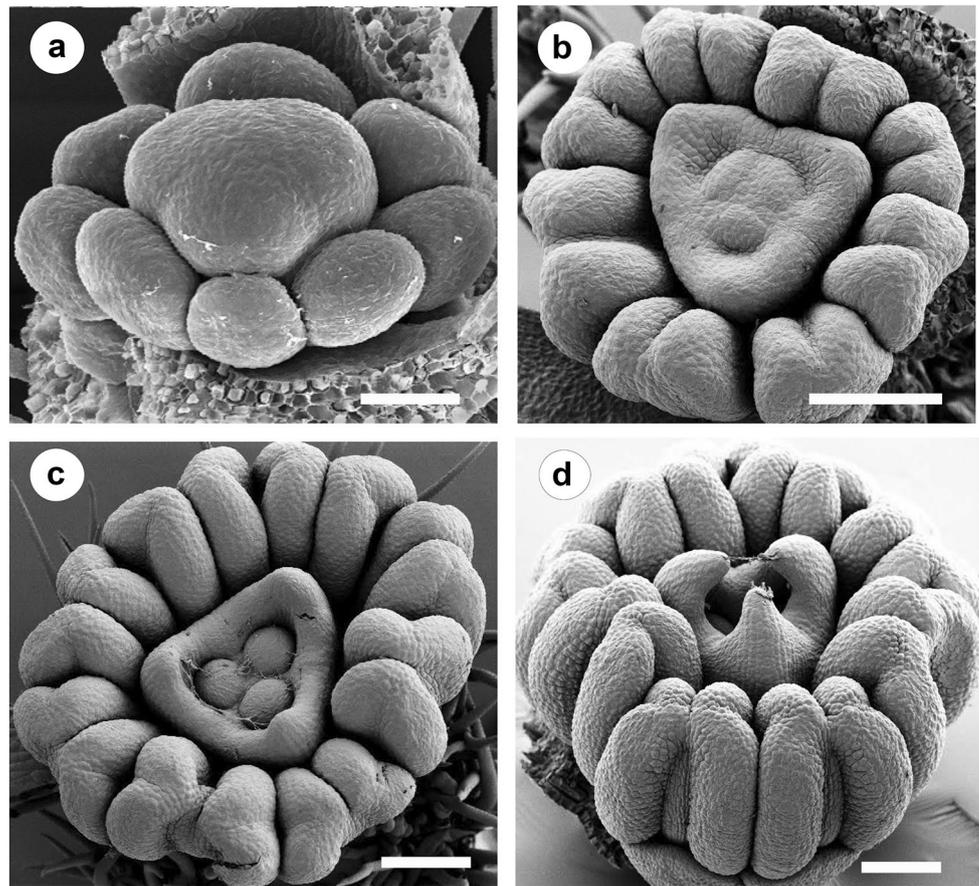
Carpels with different style positions occur in sapindalean taxa. Style position in relation to the ovary apex varies among three main types: acrostylous, anacrostylous and basistylous carpels (Weberling 1989)¹. Ontogenetic studies show that anacrostyly can be caused by an increase in the growth of the dorsal upper part of the ovary relative to the ventral part. The dorsal overgrowth leads to the formation of a dorsal bulging area in carpels which frequently hides the style base at the centre of the ovary (in multicarpellate gynoecia) at a more basal level than the ovary

apex (the style is “inserted” usually up to half-length of the ovary in sapindalean families; see Online Resource 4a; Gut 1966; Ramp 1988). In basistylous carpels the above-mentioned phenomenon is much increased so that the style is “gynobasic” close to the base of carpels (Weberling 1989). Here we highlight the groups with the last two types (anacrostylous and basistylous carpels; Table 3). In Biebersteiniaceae, some Nitrariaceae (*Tetradiclis*) and Sapindaceae (some *Deinbolia* and *Allophylus* spp.), and rarely in Rutaceae (*Zanthoxylum*, see also Table 3 in Beurton 1994) carpels are basistylous (Bachelier et al. 2011; Kubitzki 2011; Langran and Vassiliades 2008; Solís et al. 2017). Slightly anacrostylous carpels (i.e., carpels slightly bulged up on the dorsal side above the level of the base of the style) are found in some genera, such as *Peganum* (Nitrariaceae), *Homalolepsis*, *Simaba*, *Soulamea*, *Quassia* (Simaroubaceae, Alves et al. 2017; Devecchi et al. 2018; Ramp 1988) and some *Conchocarpus* spp. and *Ravenia* (Rutaceae, El Ottra et al. 2019). Strongly anacrostylous carpels (i.e., carpels abruptly bulged up on the dorsal side above the level of the base of the style, such that the style appears sunken into the ovary to different degrees, usually up to half-length of the ovary) are found in several Rutaceae (see discussion in El Ottra et al. (2019) and Ramp (1988); *Psilopeganum*, Wei et al. 2015), *Ailanthus* (Simaroubaceae, Ramp 1988), more rarely in Anacardiaceae (*Gluta*, likely *Androtium* and *Cotinus*, Wannan and Quinn 1991) and Sapindaceae (*Acer*, Peck and Lersten 1991a; *Dimocarpus*, Xu 1991; Table 3).

Other Sapindalean taxa are usually acrostylous (e.g. *Nitraria*, Nitrariaceae) but still can have dorsally bulging carpels with an apical style (Table 3; Bachelier and Endress 2008, 2009; Weckerle and Rutishauser 2005; Zhou and Liu 2012). Thus, anacrostylous and basistylous carpels may have evolved multiple times in Sapindales. Also, these features likely had “intermediate” morphological stages with acrostylous bulging carpels, as currently found in many taxa of the order (Table 3). Interestingly, ventrally bulging carpels are found in Anacardiaceae only, usually in pseudomonomerous taxa. To our knowledge, ventrally bulging carpels have not been described in angiosperms so far. In Anacardiaceae, these are acrostylous in *Solenocarpus*, slightly anacrostylous in *Blepharocarya* (Bachelier and Endress 2009; Wannan and Quinn 1991: see Fig. 19), or strongly anacrostylous in *Schinopsis* (Gonzalez 2016) and likely also in *Mycronychia*, *Loxopteridium*, *Loxostylis* and *Smodingium*, described with “lateral styles” by Wannan and Quinn (1991). It would be important to study the ontogeny of such ventrally bulging carpels, and compare them with closely related groups with the most common type of anacrostyly, that is, with dorsally bulging carpels. We believe that this unusual phenomenon may be a consequence of the reduction and integration of the sterile ovaries (and maybe

¹In acrostylous carpel the style base overtops the ovary apex (i.e., the style base is “the apical continuation of the ovary”; Weberling 1989, Fig. 4a), while in anacrostylous carpels the style base (style “insertion”, Weberling, 1989) is at a more basal level than the ovary apex (e.g., Online Resource 4, a).

Fig. 6 Early stages of the gynoecium of *Cardiospermum grandiflorum* (SEM micrographs). **a** Triangular gynoe-cium meristem with outline of three carpels. **b** Carpel walls start to develop. **c** Carpels with young ovules clearly discernable before angiospermy. **d** Carpels elongate distally, growing more extensively in its median dorsal region. Scale bars: **a** 50 μm ; **b–d** 100 μm



also of the floral apex) to the fertile carpel in the pseudomonomerous taxa, leading to the formation of a ventrally positioned bulge and to an apparent “dorsal” position of the styles. In fact, few authors noticed that anthetic flowers of *Schinus* and *Solenocarpus* have their styles displaced by the “ovary roof” or “displaced towards the dorsal side of the carpel” (Bachelier and Endress 2009).

Ontogenetic patterns of formation of the different parts of the gynoecium

“Integrative” ontogenetic studies (*i.e.*, analysis of the growth of surfaces and tissue cells) comprising the gynoecium primordium and its development up to anthesis are rare in angiosperms (Endress 1994). Still, here we tentatively describe some general patterns of gynoecium development as observed in the available studies of Sapindales (few and mostly SEM analyses), in order to provide the basis for future integrative studies. Among the Nitrariaceae, the three young carpels arise as flat and separate primordia on a common ring in *Nitraria*. The basal “ring” will develop into the syncarpous zone, but what elongates first is the young and short apocarpous zone with three primordia, which basically

corresponds to the stigma (not yet fully developed, *i.e.*, without papillae), that later fuse postgenitally (Ronse De Craene and Smets 1991). Afterwards the style and ovary elongate (the syncarpous zone). *Peganum* follows the same pattern, except that the primordia arise initially on a pentagonal meristem, that soon becomes triangular (Bachelier et al. 2011; Ronse De Craene et al. 1996). In *Kirkia* (Kirkiaceae), there is also an early formation of the apocarpous zone (Table 3), corresponding to the transition level to the base of the tapering style in early stages. Later, both the syncarpous zone below (*i.e.*, ovary), as well as the remaining parts of the apocarpous zone above elongate (*i.e.*, style and stigma). The stigmatic papillae differentiate distally (Bachelier and Endress 2008; Ramp 1988).

In Anacardiaceae, few ontogenetic series are available. Carpel meristems of *Mangifera indica* and *Anacardium humile* A.St.-Hil. (following the monomerous interpretation of the gynoecium; Bachelier and Endress 2009), arise as a ring-shaped primordium, which raises as a round-shaped ovary (the ascidiate zone; Table 3). Later it develops the style and immature stigma (plicate zone for most of its length; Tölke and Demarco 2020). *Schinus molle*, *Schinopsis balansae*, and *Pistacia lentiscus* L., with a trimerous pseudomonomerous gynoecium, have an early formation of

the single and fertile locule, as a central furrow in a dome-shaped carpel meristem (asciade zone). This is followed soon after by the development of the style and immature stigmatic region of the other two sterile carpels and the fertile one, corresponding to the apocarpous zone and future plicate zones (“incipient locules” are confined to the styles only in sterile carpels). Ovary and style elongate later in development, and after that stigmatic papillae develop. Conversely, *Spondias tuberosa* and *Tapirira guianensis* have an early formation of the plicate region of the style, followed later by the uplifting of the (syn)asciade zone, including the floral apex (Bachelier and Endress 2007, 2009; Gonzalez 2016; Tölke and Demarco 2020; Tölke et al. 2021). The unequal development of carpels, viz. with one larger (fertile) carpel primordium and two other smaller (sterile) primordia, is already discernable in young stages of the pseudomonomerous gynoecium in some taxa (before most parts of the ovary and style elongate), as seen in *Schinus*, *Schinopsis*, *Amphipterygium*, *Pistacia*, *Schinopsis* and *Rhus* (Bachelier and Endress 2007, 2009; Gallant et al. 1998; Gonzalez 2016; Hormaza and Polito 1996; Rodrigues et al. 2004; Tölke and Demarco 2020). Thus far, except for *S. tuberosa* and *T. guianensis* in Anacardiaceae the asciade zone is the first part to be formed in gynoecium development, regardless whether the taxon is monomerous or pseudomonomerous (in the later, the fertile asciade locule is the first to be formed).

In Sapindaceae, more detailed information of early carpel development is available. The carpel meristem is usually triangular, reflecting the trimerous merism common in the family (with few exceptions, such as Acereae, where are generally dimerous, as in most *Acer* and *Dipteronia*, and among Sapindoideae found in *Deinbollia grandiflora* Hook.f.; Ronse De Craene 2010, unpubl. data; Zhang 2018). Young carpels arise as separate primordia (*Xanthoceras*, *Aesculus*, *Acer*, *Eurycorymbus*, *Litchi*, *Dimocarpus*), or separate on a common basal meristem (that later elongates into the syncarpous zone; *Koelreuteria*, *Delavaya*, *Cardiospermum halicacabum* L., and apparently in *Handeliidendron*), or even as a continuous basal ring meristem (*Serjania*) (Cao and Xia 2009; Cao et al. 2006, 2017, 2018; Peck and Lersten 1991a; Ronse De Craene et al. 2000; Ronse De Craene unpubl. data; Fig. 6a, b; Ronse De Craene and Haston 2006; Xu 1990, 1991; Zhou et al. 2019).

Among the Acereae, *Dipteronia* develops an early apocarpous zone, followed by an early symplicate zone (Zhang 2018). *Acer saccharum* is unusual in having young naviculate carpels, corresponding to the early apocarpous zone, that remains open for several months. Carpels continue to grow, initially more extensively in the median dorsal region, and close only in spring, forming the basal syncarpous zone and the rest of the apocarpous zone distally (the style/stigma; Peck and Lersten 1991a). A similar developmental pattern was found in the young gynoecium of

Cardiospermum (Sapindoideae, Paullinieae, Fig. 6b–d), with carpels also remaining open for a long time. *Eurycorymbus* is also unusual in having rounded erect reniform carpel primordia, corresponding to the early apocarpous zone. In a later stage the three young carpels elongate and meet at the centre, forming “three terminal slits” that correspond to the young stigmatic region that is later uplifted by style elongation. A similar pattern of stigma development was also observed in *Koelreuteria* species (Cao et al. 2017, 2018; Ronse De Craene et al. 2000). For *K. paniculata* information is available for the ovary development, as the ovary enlarges above the level of the placenta through intercalary growth as a “tube”, growing upwards (Ronse De Craene et al. 2000). The stigmatic papillae differentiate usually in mature gynoecea in Sapindaceae, except for *K. bipinnata* and *Dimocarpus*, where immature (short) papillae are present in young carpels before style elongation (Cao et al. 2018; Xu 1991).

In Simaroubaceae, ontogenetic series are available for *Quassia amara* and *Ailanthus glandulosus*. Their gynoecea are mostly apocarpous. The young apocarpous ovary is the first part of carpels to be formed in *A. glandulosus* (Table 3). In a later stage the young carpels elongate and meet distally at the centre to elongate into the style and fuse postgenitally. Stigmatic papillae differentiate distally. *Q. amara* has a similar development, except that the young carpels share a common base from early stages (*i.e.*, before carpel closure), that corresponds to the young gynophore (Endress et al. 1983; Ramp 1988).

Among the Rutaceae there is a greater amount of detailed ontogenetic studies with SEM and light microscopy analyses (*e.g.*, El Ottra et al. 2013, 2019; Gut 1966; Ramp 1988; Wei et al. 2011, 2015). Apocarpous Rutoideae share the same developmental pattern of the Simaroubaceae gynoecium (Table 3) and in some taxa, young carpels share a common base from early stages, that corresponds to the young gynophore or to the short congenitally fused ovary base (El Ottra et al. 2013, 2019; Endress et al. 1983; Gut 1966; Ramp 1988; Wei et al. 2015).

Among the syncarpous Rutaceae, four main patterns could be found in Rutoideae. The first is similar to the apocarpous Rutoideae in that the young apocarpous zone of carpels is the first part to elongate, corresponding to the upper part of the ovary followed by style elongation (in *Calodendrum*, *Phellodendron*, *Clausena*, *Ruta*, *Skimmia*, *Coleonema*, *Haplophyllum*). Eventually young carpels also share a common base from early stages (before style formation), as in *Clausena*, *Ruta*, *Skimmia*, *Coleonema* and *Haplophyllum*, which later elongates as the syncarpous zone (Gut 1966; Ramp 1988; Wei et al. 2015). The second pattern was found for bicarpellate *Ptelea*, and apparently in *Psilopeganum* (but developmental stages are missing for the later), where the syncarpous zone of the ovary appears first as a furrow in the centre of the gynoecium meristem. Also, a median slit

divides the meristem distally in two. Next the young carpels elongate into a young style and immature stigmatic region (short and distal apocarpous zone of the mature gynoecium). In a later stage the ovary elongates, with further elongation of the style (Gut 1966; Ramp 1988; Wei et al. 2011). A third pattern was found in *Murraya* (Aurantieae) where the two young carpels arise as separate primordia, corresponding to the early formation of the short and distal apocarpous zone, which basically corresponds to the stigma in later stages. Afterwards the syncarpous zone, which comprises most part of the gynoecium (style and ovary), elongates below as a tube, with a later expansion of the ovary (Ramp 1988; Wei et al. 2015). Finally, the fourth pattern is restricted to *Citrus* (Aurantieae) which is unusual among the family in having a multicarpellate gynoecium (Endress 2014). At first the young syncarpous zone appears as a large dome-shaped meristem, concave at its centre, with several narrow slits radially arranged at its inner borders (the congenitally fused carpel primordia, one slit per carpel). In *C. sinensis* these slits differentiate the styler canals first, and later enlarge at the base forming the ovary locules (Gut 1966). Carpel flanks gradually develop upwards, and distally a symplicate zone is observed, followed by the formation of a short apocarpous zone, that is restricted to the stigma in *Citrus*. Carpel flanks develop slightly unequally at the tips and do not form a regular circle (in species with one or two whorls of carpels; Gut 1966; Lord and Eckard 1985; Ramp 1988), a common phenomenon found in multicarpellate angiosperms due to lack of space (Endress 2014). Stigmatic papillae usually differentiate in mature gynoecia in Rutaceae, except for *Cneorum tricoccon* (Cneoroideae) and *Boronia spathulata* Lindl. (Rutoideae, Boronieae), where immature (short) papillae are present in young carpels (at initial stages of style elongation; Caris et al. 2006; Ramp 1988).

In Meliaceae, few ontogenetic studies are available, and a more complete ontogenetic series is described for *Trichilia pallens* for the first time in this review (Fig. 5; Table 3). In *T. pallens* the three carpel primordia arise as horseshoe-shaped primordia which basically correspond to the very tips of the stigma in later stages (Figs. 4b and 5a). Soon after carpels share a common base that elongates as a tube for the entire syncarpous gynoecium, *i.e.*, the rest of the stigma, style and ovary (apparently first as the symplicate zone; Fig. 5b, c). In later stages the ovary expands in a globular structure (Fig. 4e, f). Interestingly, the stigmatic region differentiates very early in the gynoecium development, *i.e.*, before style elongation. Young and short stigmatic papillae are already seen at this stage, with further elongation of the papillae occurring later (Fig. 5b–e). Other genera of Meliaceae apparently have a different pattern of gynoecium development. *Cedrela odorata* and *C. fissilis* have five carpel primordia (as five small protuberances) at each vertex of the pentagonal gynoecium meristem. Later

the basal syncarpous zone as well as the distal apocarpous zone develops, the latter corresponding to the distal part of the style and stigma. The development of the large papillate stigmatic head occurs in later stages (after the initial style elongation; Gouvêa et al. 2008a). Therefore, this comparative ontogenetic analysis indicates that the gynoecium of Meliaceae taxa studied so far share more similarities with some Rutaceae, and not with Simaroubaceae. In the case of *T. pallens* it is similar to the third pattern of the syncarpous gynoecium found in Rutaceae, and *Cedrela* may be similar to the first pattern, though ontogenetic stages are missing for a proper comparison in this taxon. Also, an early differentiation of the stigmatic papillae, as found in *T. pallens*, is highly unusual in the order, found elsewhere only in a few Rutaceae and Sapindaceae. In fact, other Meliaceae are described as having a late differentiation of stigmatic papillae (*Cedrela*, *Toona* and *Swietenia*, Gouvêa et al. 2008a, b).

Regarding the patterns of development of angiospermy, Sapindales representatives mostly have early carpel closure, since ovules are not seen from the outside in young stages, similar to the majority of angiosperms. Only three exceptions are found in the order, where a delayed carpel closure enables to see ovules externally before angiospermy: *Acer saccharum*, *Cardiospermum halicacabum* (Fig. 6c, d; Sapindaceae: Peck and Lersten 1991a) and *Pistacia vera* L. (Anacardiaceae: Endress 2015; Takeda et al. 1979). Also, in *Skimmia japonica* Thunb. the placentae are visible in carpels proceeding to angiospermy (Ramp 1988: see Fig. 114).

Stigmatic features

Although stigmatic features can be highly variable in Sapindales, we highlight important features that characterize taxonomic groups, or common patterns of variation in the order that are likely apomorphic tendencies. In all Nitrariaceae (Bachelier et al. 2011) and in several Sapindaceae the stigmatic region, as seen from the surface, is formed by stigmatic papillae distributed along the lateral fused margins of each carpel, forming receptive grooves that run from the tip of the stigma downwards to variable levels. These grooves are usually long in *Koelreuteria* species (stigmatic papillae spread as lines along each carpel up to the lower half of the style, Avalos et al. 2019; Cao et al. 2018; Ronse De Craene et al. 2000), *Averrhoidium*, and *Peganum* (Nitrariaceae; Bachelier et al. 2011; Table 3). The grooves are shorter in other groups, such as in *Xanthoceras* (early diverging Sapindaceae; Zhou et al. 2019), *Magonia* (González et al. 2017), *Paullinia clavigera* (Weckerle and Rutshausen 2005), and probably in *Eurycorymbus* (Cao et al. 2017). Each lateral “line” of the stigmatic region alternates with a non-papillose (and probably non-receptive) dorsal area (*e.g.*, Fig. 1a, i'; Table 3). This feature was described separately before for

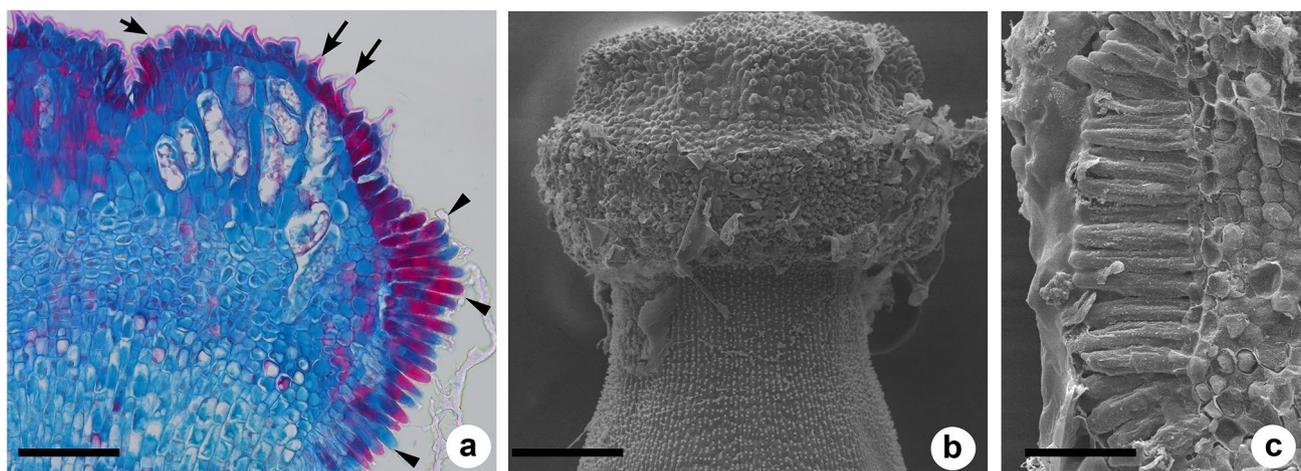


Fig. 7 Stigma of *Trichilia pallens* (Meliaceae). **a** Photomicrograph of a detail of a longitudinal section; note the thick cuticle in the upper short-papillate area (arrows), and trichomes in the lower lateral area (arrowheads). **b**, **c** SEM micrographs of the cylindrical stigma,

showing the two-parted arrangement of the stigmatic cells (papillae/trichomes). **c** Detail of a sectioned stigma, exposing the lateral trichomes, covered with secretion (also observed **a**, arrowheads, and **b**). Scale bars: **a** 100 μ m; **b** 200 μ m; **c** 50 μ m

both families, but using a different terminology (see family descriptions in Acevedo-Rodríguez et al. (2011), and Stevens (2001) onwards) Since the positions of Nitrariaceae and Sapindaceae are still not resolved with confidence in the phylogeny of Sapindales (Muellner-Riehl et al. 2016; Stevens 2001 onwards), the flower structure of both families should be comparatively studied in more detail, along with other features. However, in Sapindaceae another common type of stigma structure is the one with long and free stigmatic branches (usually three or two), covered with papillae on the adaxial side (lateral and ventral surfaces of unfolded carpels; Table 3).

Unicellular stigmatic papillae are common and widespread in Sapindales (Bachelier et al. 2011). They are currently found in all Nitrariaceae (Bachelier et al. 2011; Ronse De Craene and Smets 1991), most Rutaceae (El Ottra et al. 2019), Simaroubaceae (Alves et al. 2017; Ramp 1988;), Sapindaceae (Avalos et al. 2019; Cao et al. 2018; Peck and Lersten 1991a, b; Ronse De Craene et al., 2000; Weckerle and Rutshausen 2003, 2005), Meliaceae (Gouvêa et al. 2008a, b; this study, Fig. 7a). “Uniseriate multicellular papillae” are commonly found on stigmas of the closely related families Anacardiaceae, Burseraceae and Kirkiaceae and thus this is an apomorphic tendency for this clade (Bachelier and Endress 2008, 2009; Gonzalez 2016; Tölke and Demarco 2020). Bicellular “hairs” can be occasionally found on the stigma of *Trichilia catigua* and *T. pallida* of Meliaceae (Souza et al. 2001). We believe that the above mentioned “multicellular papillae” and “hairs” would be better termed as trichomes, based on their multicellularity (Table 3).

Non-papillose smooth stigmas are rarely reported in Sapindales. They occur in few Rutaceae (El Ottra et al. 2019; Heslop-Harrison and Shivanna 1977; Ramp 1988),

Simaroubaceae, and Sapindaceae (Heslop-Harrison and Shivanna 1977). Due to the variable degrees of sterility among gynoecea of unisexual flowers of Sapindales, stigmas have been previously erroneously described as non-papillose in some species of *Acer* (Sapindaceae), based on observations of poorly developed carpelodes (Peck and Lersten 1991b, contradicting findings of Heslop-Harrison and Shivanna 1977). In fact, carpelodes can have collapsed or degenerated papillae in *Acer*, *Xanthoceras* (Sapindaceae; Yadav et al. 2016; Zhou et al. 2019) and *Ailanthus glandulosus* (Simaroubaceae; Ramp 1988), or are described as “undifferentiated” in *Spondias macrocarpa* (Anacardiaceae, Tavares et al. 2020).

Unicellular papillae are usually short in Sapindales, though “long unicellular papillae” or “hairs” have also been described. Gouvêa et al. (2008a, b) considered that “long papillae” are present only on the “underside” of the “capitate” stigma of *Cedrela*, *Toona* and *Swietenia* species (Meliaceae). In fact, in Meliaceae stigmas are commonly described as having “hairs” instead of papillae. Stigmas with long unicellular “hairs” were described by Narayana (1958), for *Swietenia*, and by Nair (1963), for *Toona* (both Cedreloideae). In Melioideae the same was found for *Azadirachta*, *Melia*, *Aglaia*, *Soymida*, *Hynea*, *Walsura*, *Turrea* (only at the upper side of the cylindrical stigma in the latter taxon; Murty and Gupta 1978a, b; Narayana 1958, 1959).

A more detailed description of the stigma exists for other Melioideae, such as *Guarea* and *Trichilia* (Souza et al. 2001, 2002; this study). In *Trichilia catigua* and *T. pallida* there are two types of stigmatic “hairs”, with unicellular more frequent than bicellular hairs (*i.e.*, trichomes). For *Guarea*, two types of “unicellular papillae” were found: a short one, positioned at the upper side of the cylindrical stigma, and a long one (*i.e.*, trichomes) positioned in the lateral area of

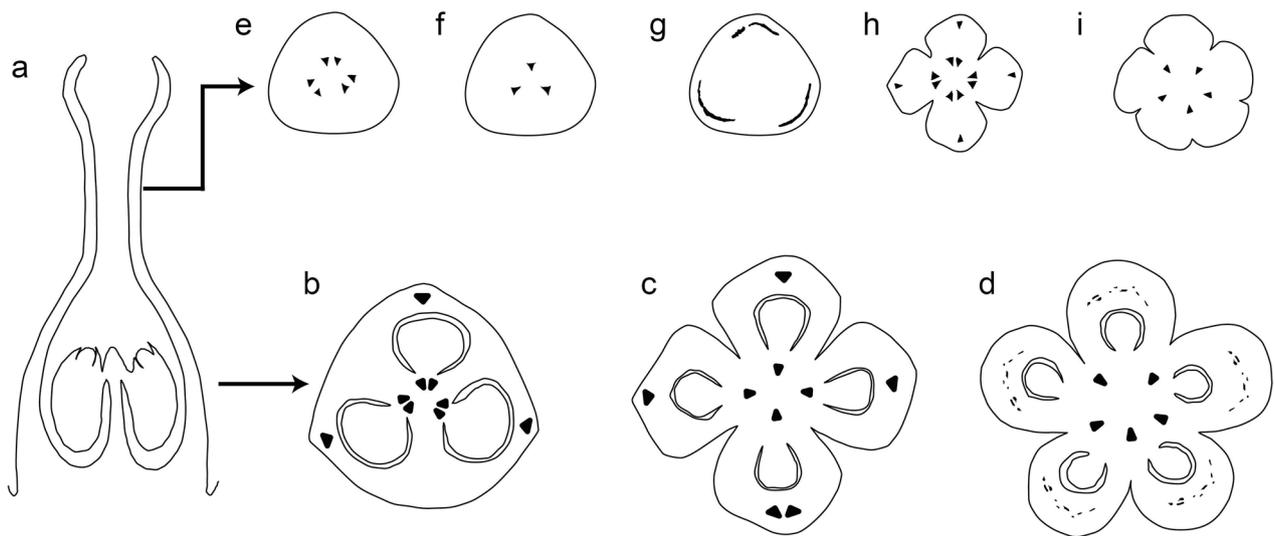


Fig. 8 Main patterns of gynoecium vascularization in Sapindales (thin lines correspond to morphological surfaces; dark shading indicates vascularization). **a** Schematic median longitudinal section of gynoecium (arrows indicate the level of cross sections schemes). **b–d** Schematic transsections at the ovary level, showing: **b** one main dorsal bundle and two main ventral (lateral) bundles per carpel; **c** one (or two) main dorsal and ventral vascular bundle per carpel; **d** diffuse and reticulated dorsal vasculature plus five synlateral bundles of carpels (each one shared by adjacent carpels). **e–i** Schematic transsections at

the style level, showing: **e** two free ventral (lateral) bundles per carpel; **f** single (fused) ventral per carpel; **g** one (or more) band(s) of vascular tissue per carpel; **h** one dorsal plus two ventrals per carpel; **i** five synlateral bundles. Based on: Weckerle and Rutishauser 2005 (b); Bachelier and Endress 2008; Alves et al. 2017 (c); El Ottra et al. 2019 (d); Ronse De Craene et al. 2000 (e); Weckerle and Rutishauser 2003 (f); Bachelier et al. 2011 (g); Wannan and Quinn 1991 (h); and Ramp 1988 (i)

the stigma. This was similar for *Trichilia pallens*, with some differences. The upper stigmatic papillae are not only short, but also covered by a thick cuticular layer, occurring also in the upper lateral area of the cylindrical stigma (Fig. 7a). In the lower lateral areas of the stigma much longer trichomes occur. These trichomes do not have a thick cuticle but are covered by stigmatic secretions instead (Fig. 7b, c). We believe that this lower region of the stigma is its receptive area. This idea was also put forward by Gouvêa et al. (2008a) and tested by Gama et al. (2021b), who observed that no pollen was seen germinating on the upper side of the stigma in other Meliaceae taxa. However, some angiosperms can have the cuticle rupturing on the stigma due to insect activity, turning the stigma receptive (Owens 1989). Alternatively, this lower lateral area could be a secondary pollen presentation site, as found in other groups of Melioideae (*Naregamia* and *Turraea* spp.: Yeo 1993). Further functional studies are needed to test these ideas. Such two-parted positional pattern of size differentiation in stigmatic cells was found nowhere else in Sapindales (Fig. 7b).

Patterns of gynoecium vascularization

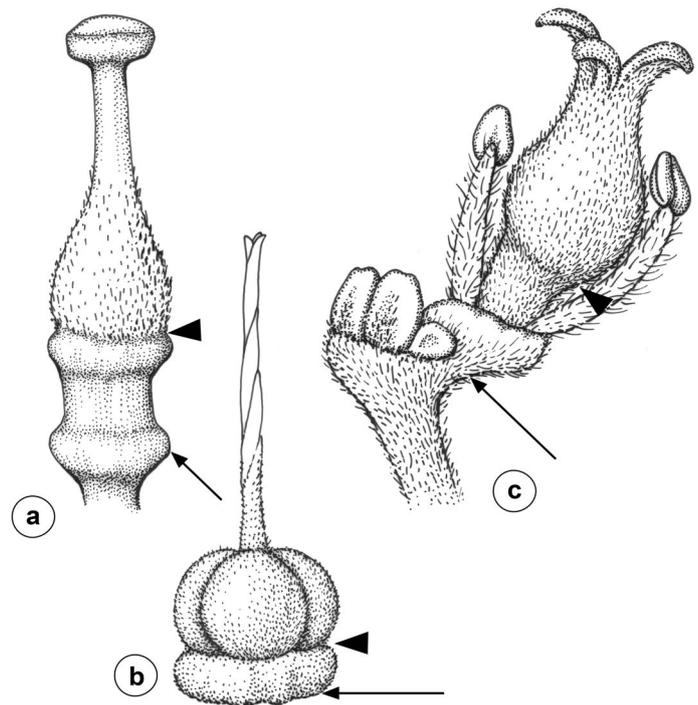
Vascular bundles of the gynoecium exhibit a wide variety of structural features in angiosperms, related to positional, quantitative and histological variations. It is stated

that vascular bundles are “formed where they are needed” (Endress 2019). Complex patterns of gynoecium vascularization have been frequently described for Sapindales (e.g., Bachelier and Endress 2009, Bachelier et al. 2011; Ronse De Craene and Haston 2006). Though vascularization features are highly variable, Ronse De Craene and Haston (2006) comparatively analysed some of the vascular features of the gynoecium in Sapindales.

Herein we highlight some general patterns that could be recognized in this and other studies, related to positional and quantitative features of vascularization.

In Sapindales, a correlation seems to exist between the amount of lateral vascular tissue and the size of the anthetic gynoecium (El Ottra et al. 2019), or with the thickness and texture of the pericarp in fruiting carpels (Weckerle and Rutishauser 2005). This was also found in other angiosperms (Carlquist 1969; Endress 2019). When comparing the small gynoecium of *Ertela* with other large-flowered Galipeinae (Rutaceae), it is noticeable that the numerous additional lateral bundles that are so widespread in the subtribe are absent in the former (El Ottra et al. 2019). Also, when comparing the anthetic gynoecium of Paulliniaceae (Sapindaceae), it is clear that the “dense network of secondary lateral vascular bundle” is reduced only in taxa where fruiting carpels develop thin, dry, papery pericarps (in *Cardiospermum*, *Urvillea*, and *Serjania* species: Weckerle and Rutishauser 2005). Similarly in *Leitneria* (Simaroubaceae; Abbe and

Fig. 9 Morphology of gyno-
phores in Sapindales: **a** *Guarea*
(Meliaceae); **b** *Iridosma*
(Simaroubaceae); **c** *Paullinia*
(Sapindaceae). Arrows indicate
perianth level, which has been
omitted; arrowhead indicate the
upper end of the gynophore.
Modified from Pirani (1992)
(a), Aubréville (1962) (b), and
Acevedo-Rodriguez and Som-
ner (2018) (c)



Earle 1940) the single carpel that later forms a drupe filled with air cavities and a thin dry pericarp, also presents a reduced lateral vascular system compared to other Simaroubaceae (Alves et al. 2017; Nair and Joseph 1957; Nair and Joshi 1958; Ramp 1988).

Although a broadly reticulate vascular system is commonly observed in Sapindales, especially in the ovary, some positional and quantitative patterns could be recognized in the median dorsal and ventral region of the carpels, and these variations are presented in Fig. 8a–d, and in Table 3 for each family. The more common vascular pattern found in the dorsal region of the ovary in families of Sapindales is the one where a main median dorsal bundle is absent for most of the length of the ovary², and instead a “diffuse” and “weakly differentiated” dorsal vasculature predominates (Table 3; Fig. 8d; Avalos et al. 2019; Bachelier and Endress 2008, 2009; Bachelier et al. 2011; El Ottra et al. 2019; Gut 1966; Murty and Gupta 1978a; Nair 1963; Narayana 1958, 1959, 1960a, b; Pirani et al. 2010; Ramp 1988; Ronse De Craene and Haston 2006; Ronse De Craene et al. 2000; Souza et al. 2002; Tölke and Demarco 2020). Since “well-developed”

dorsals are considered a plesiomorphic feature for the malvid clade, and considering that Malvales also have “dorsals that are weakly developed” (or lost; Ronse De Craene and Haston 2006), this feature could be an apomorphic tendency shared by Sapindales and Malvales (Table 3).

In relation to patterns observed for vascular bundles in or close to the ventral region of carpels, three main patterns were found at the ovary level, as presented in Table 3 and Fig. 8b–d. Apparently, the latter pattern, synlateral bundles running for most of the ovary length (Fig. 8d) could be an apomorphic tendency for the Meliaceae as it has been found in most of its taxa so far, but is also shared with some Rutaceae (Table 3). In fact, two free ventral bundles for most of carpel length (first pattern mentioned above, Fig. 8b), is plesiomorphic for Sapindales (Ronse De Craene and Haston 2006).

In relation to the vascularization in the region of the style and running for most of its length, five main patterns were found, and these are presented in Fig. 8e–i, and in Table 3. Dorsal bundles running as broad bands of vascular tissue in the style (Fig. 8g; Bachelier et al. 2011) are likely an autapomorphy for Nitrariaceae (Table 3). In contrast to the dorsal vasculature (Fig. 8d), the vascular bundles at the ventral region of carpels, including the style and ovary, are in general well developed for Sapindales (Fig. 8b–f, i). This condition is also present in Malvales and thus likely an apomorphic tendency (*sensu* Endress and Matthews 2012) shared by these two families. In the style, the presence of well-developed ventral bundles for most of its length is a

² Some Sapindaceae with one conspicuous main median dorsal bundle and a triangular-shaped ovary have a dorsal wing in the same region (*Dodonaea*, Paoli and Sarti 2008), or at least a dorsal rib in the antheticgynoecium, that will develop later into the wings of fruitlets (many Paullinieae; Weckerle and Rutishauser 2005). Differently, other Sapindaceae with similar ovary shape (*Koelreuteria*), but with deepdehiscence lines (furrows) in the median region, dorsal bundles are absent (Avalos et al. 2019; Cao et al. 2018; Ronse De Craene et al. 2000).

putative synapomorphy for Sapindales (Ronse De Craene and Haston 2006).

Gynophores and androgynophores

Gynophores or androgynophores occur in flowers of all families of Sapindales. Gynophores are much more widespread and common in the order, also frequently found in flowers of other malvids (Table 3; Endress and Matthews 2006). Gynophores in Sapindales may have variable length and shape. In Biebersteiniaceae and Kirkiaceae gynophores are short (Bachelier and Endress 2008; Muellner 2011). In Nitrariaceae, *Peganum* has a short and slender gynophore (Bachelier et al. 2011). Anacardiaceae rarely have gynophores, found in *Gluta*, *Actinocheita* (Pell et al. 2011), *Anacardium* (Ronse De Craene and Haston 2006), and *Dracontomelon* (short and slender, Bachelier and Endress 2009). Though gynophores are not commonly found in Sapindaceae, they were described in *Conchopetalum* (Acevedo-Rodríguez et al. 2011). In *Handeliidendron* a short and stout gynophore can be observed (Cao et al. 2006). *Averrhoidium* has a very short constriction below the ovary (Weckerle and Rutishauser 2003). Additionally, gynophores are likely present in species of *Cossinia*, *Delavaya*; *Loxodiscus*, *Majidea*, *Nephelium lappaceum*, *Paullinia*, *Serjania* (Fig. 9c; Weckerle and Rutishauser 2003, 2005), *Dodonaea*, *Houssayanthus*, *Lophostigma* (Solís et al. 2017), and *Lepisanthes* (Acevedo-Rodríguez et al. 2011) since these taxa are described as having a stipitate gynoecium. In Simaroubaceae, conspicuous gynophores are widespread, and considered to have evolved once in the family, but with multiple reversals (Devecchi et al. 2018). It is found in *Brucea* (short, Letneriaceae: Nair and Joshi 1958), *Simaba*, *Homalolepsis*, *Quassia*, *Hannoa*, *Iridosma*, and *Samadera* (Fig. 9b; Simaroubaceae: Devecchi et al. 2018; Engler 1931; Nair and Joseph 1957; Ramp 1988). Similarly, in Meliaceae gynophores occur in many taxa, having evolved independently four times or more. It is found in taxa of both subfamilies such as *Chukrasia* (Cedreloideae), *Guarea*, *Heckeldora*, *Trichilia*, *Chisocheton*, *Ruagea*, *Megaphyllaea*, *Schmardaia* (Meliaceae; Gama et al. 2021a; Mabblerley 2011; Pennington and Styles 1975; this study Figs. 4a and 9a). In *Trichilia pallescens*, it is a short and protuberant gynophore, larger than the locule bases. In Rutaceae, gynophores are also commonly found, present in all subfamilies and most tribes (Kubitzki et al. 2011), with a variety of shapes and sizes. They can be thin and very long, distally broad and gradually narrowing proximally, as in *Spiranthera* (J.H.L. El Ottra pers. obs.); or long and slender, as in *Calodendrum* and *Boenninghausenia* (Ramp 1988; Wei et al. 2015); or long and rounded (*Ptelea*). Gynophores are short and stout in many taxa, or very short (El Ottra et al. 2019; Gut 1966; Ramp 1988). Gynophores

in Rutaceae, Simaroubaceae and Meliaceae are considered a homoplastic and derived feature, due to their variability in shapes, sizes and phylogenetic distribution (Devecchi et al. 2018; Gama et al. 2021a; its evolution was not evaluated for Rutaceae so far, Table 3).

In contrast, androgynophores are not widespread in Sapindales, and likely also a homoplastic and derived feature. They have been described in a few taxa of Burseraceae (Garugeae, in *Canarium*: Daly et al. 2011), Sapindaceae (Hippocastenoideae, in *Koelreuteria*: Avalos et al. 2017; Cao et al. 2018; Ronse De Craene et al. 2000; Sapindoideae, in *Urvillea*, *Ungnadia*: Acevedo-Rodríguez et al. 2011; *Paullinia* spp.: Lima et al. 2016; Perdiz et al. 2012; *Cardiospermum* spp.: Zini et al. 2014), Simaroubaceae (Ailanthaceae, in *Ailanthus*: Ramp 1988), Meliaceae (only in Cedreloideae, tribe Cedreleae, in *Cedrela* and *Toona*: Gouvêa et al. 2008a; Gama et al. 2021a), and Rutaceae (Cneoroideae, in *Cneorum*: Caris et al. 2006). Gynophores or androgynophores can be usually associated with the presence of nectary tissue, usually developing late at its periphery as a protuberant tissue of variable shapes (e.g., Alves et al. 2017; Cao et al. 2018, Caris et al. 2006; El Ottra et al. 2019; Gut 1966; Ramp 1988; Ronse De Craene et al. 2000; Solís et al. 2017). If we consider the androgynophore as a derived feature, then it could be an apomorphic tendency shared by the families Burseraceae, Sapindaceae, and the clade Meliaceae, Simaroubaceae and Rutaceae (Table 3).

Despite the large variety of gynophores found, two main types can be recognized in detailed structural studies:

- (1) As a floral internode derived from intercalary growth between the gynoecium and androecium. A distinct constriction below the ovary is found and indicates the upper level of the floral internode (i.e., upper level of the gynophore). This is found in *Ptelea*, *Zanthoxylum*, *Murraya* (Rutaceae: Gut 1966; Ramp 1988). In Simaroubaceae this internode may be quite conspicuous (Fig. 9b; in Alves et al. 2017: see there Fig. 5g, and in Devecchi et al. 2018: see there Fig. 1n, o). The distal end of the gynophore may be flat (several *Homalolepis* and *Simaba* species, *Hannoa*, *Gymnostemon*, *Pierreodendron*, *Eurycoma*, *Perriera*, *Picrolemma*, *Quassia*) or “with an undulate rim surrounding the ovary base” (few *Simaba* species: Devecchi et al. 2018; *Brucea*: Nair and Joshi 1958). Thus, this kind of gynophore is a marked feature of Simaroubaceae, likely an apomorphic tendency, but shared with some Rutaceae. Morphological analysis indicates that *Guarea* (Meliaceae) may also have this type of gynophore (Fig. 9a).
- (2) The second type of gynophore is also formed by intercalary growth, but at the base of the ovary locules, and thus morphologically the gynophore is a sterile part of the gynoecium, and no constriction is found, except at

the gynophore base (*i.e.*, the gynoecium base). This occurs in Kirkiaceae (Bachelier et al. 2008); Anacardiaceae (*Dracontomelon*: Bachelier and Endress 2009), Rutaceae (several genera: El Ottra et al. 2013, 2019; Gut 1966; Ramp 1988; Wei et al. 2011, 2015), and Meliaceae (*Guarea*: Souza et al. 2002; *Trichilia*, this study Fig. 4a), and thus appears to be the most common type in Sapindales. *Ailanthus* (Simaroubaceae), has an unusual androgynophore that can combine both types of gynophore mentioned above (see Fig. 14 in Endress et al. 1983, and Fig. 23h in Ramp 1988). In fact, it is not always easy to discern in a flower what is derived from the floral apical meristem, or what is “a developmentally secondary structure” like a floral internode (Endress 2019). Additionally, gynophores and androgynophores can be interpreted as extensions of the floral receptacle and the result of intercalary growth (Ronse De Craene 2010). Detail ontogenetic information on gynophores is needed in order to clarify its origin(s).

Conclusions

Our study is a broad comparative account of the gynoecium structure of Sapindales in the current phylogenetic context of relationships of its nine families. We found that some gynoecium features are broadly shared among its families and thus likely apomorphic tendencies (*sensu* Endress and Matthews 2012). We found this to apply to following characters:

- (1) Stigmas with lateral receptive papillose (commissural) lines running downwards in each carpel to variable levels, and a similar PTTT structure are found in Nitrariaceae and Sapindaceae (Avalos et al. 2019; Bachelier et al. 2011; Cao et al. 2018; Ronse De Craene and Smets 1991; Ronse De Craene et al. 1996, 2000; Weckerle and Rutishauser 2003; Zhou et al. 2019). Considering all available evidence to date, stigmatic features should be studied in more detail in Sapindaceae as they appear to have systematic importance. Additionally, the floral apex is not an integrated part of the gynoecium architecture in Sapindaceae and Nitrariaceae, and thus this could be an ancestral condition shared between these families (Table 3).
- (2) The clade comprising Burseraceae, Kirkiaceae and Anacardiaceae share features such as multicellular stigmatic trichomes, and many others already listed by Bachelier and Endress (2008, 2009).

More rarely, other features were found exclusively in single families, such as ventrally bulging carpels in pseudomonomerous Anacardiaceae (Bachelier and Endress 2009; Gonzalez 2016; Wannan and Quinn 1991), and half-open

PTTT in Sapindaceae. In Meliaceae a two-parted pattern of distribution of long trichomes and short/thick stigmatic papillae was found (Souza et al. 2002; this study).

In relation to the yet disputed trichotomy involving Meliaceae, Rutaceae and Simaroubaceae (Stevens 2001 onwards) we found features that favour a closer relationship of Rutaceae to Simaroubaceae, such as: a mostly apocarpous gynoecium with the young ovary developing earlier than other parts, absence of the symplicate zone; fruits separating as fruitlets from early stages; a “closed” PTTT positioned in the inner angles of the postgenitally fused ventral slit at the plicate zone of carpels, a floral apex enclosed within the ovary base, and smooth stigmas (Table 3). Alternatively, we found features that favour a closer relationship of Meliaceae to Rutaceae (mostly present in syncarpous Rutoideae, Aurantieae), such as: stylar canals, two similar patterns of gynoecium development, synlateral vascular bundles for most of the ovary length; and gynophores derived from the gynoecium, that are not constricted distally. Both hypotheses of relationship have been retrieved in previous phylogenetic studies (*e.g.*, Gadek et al. 1996; Lin et al. 2018), while the sister relationship between Simaroubaceae and Meliaceae has been also retrieved with moderate support (Muellner-Riehl et al. 2016). No gynoecium feature presented in this study supports this last relationship.

Other features are likely apomorphic tendencies of Sapindales, such as a postgenitally fused stigmatic head (Bachelier and Endress 2008, 2009; Bachelier et al. 2011) and a floral apex forming an integrated part of the gynoecium, as in Biebersteiniaceae, Kirkiaceae, Anacardiaceae, Burseraceae, Simaroubaceae, and Rutaceae (Bachelier and Endress 2008, 2009; El Ottra et al. 2013, 2019; Gut 1966; Ramp 1988; Yamamoto et al. 2014; this study). Other apomorphic tendencies are shared with Malvales within malvids, related to recognized main vascularization patterns (Ronse De Craene and Haston 2006).

Gynoecium traits may be unusually developmentally complex (Endress 2019) and therefore, it is important that modern studies integrate both scanning electron and light microscopic analyses throughout gynoecium development, in order to precisely recognize gynoecium features in comparative and evolutionary studies. We partially integrated such available studies, but also highlighted the gaps that still need to be filled for Sapindales.

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